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# Journal canadien des sciences halieutiques et aquatiques

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# Introduction to the International Workshop on Lobster Recruitment

Alan Campbell

*Department of Fisheries and Oceans, Fisheries Research Branch, Invertebrates and Marine Plants Division, Biological Station, St. Andrews, N.B. E0G 2X0*

During 1977, an international "Workshop on lobster and rock lobster ecology and physiology" hosted by CSIRO was held in Perth, Western Australia (Phillips and Cobb 1977). A major area recognized by the workshop participants that required further research was recruitment in lobster populations. Since 1977, various countries sponsored research into lobster recruitment. Much of the information remained largely unconsolidated. Consequently, another international workshop was planned as a forum to examine aspects of lobster biology relevant to lobster recruitment.

Recruitment is defined, for the International Workshop on Lobster Recruitment, as *the number of progeny derived from a spawning population surviving to a subsequent defined life stage*. Recruitment is controlled by a complex of factors. For example, the location and size of brood stock (number of eggs), larval distribution in relation to oceanographic phenomena, location and magnitude of larval settlement, and the behavioral and population ecology of juveniles are some factors that affect lobster recruitment. Understanding recruitment mechanisms would improve substantially the predictive capability of models for forecasting lobster population size and composition and, consequently, benefit fisheries resource management.

The Workshop objective was to convene active lobster research scientists from throughout the world to review and compare recent studies on the influence of biological and environmental processes on lobster stock recruitment, to provide a perspective of how field and laboratory results (past and present) can be integrated into (1) the development of models of recruitment mechanisms and population control and (2) management strategies for valuable lobster resources, and to identify future research requirements on recruitment.

Most participants were invited, the number being restricted in an attempt to permit a workshop environment. To increase interdisciplinary communication, crab and crayfish biologists were invited as workshop participants in part because (a) some crab species of commercial importance occupy similar environments and have life history stages similar to those of lobsters, (b) problems in studying recruitment in crabs and crayfish are similar to those of lobsters, and (c) crab and crayfish recruitment is better understood than lobster recruitment in some areas.

The International Workshop on Lobster Recruitment was held at the Algonquin Hotel, St. Andrews, New Brunswick, Canada, during 1–5 July 1985. Eighty-eight papers were presented (68 verbal and 20 posters) over the first four days. Eight consecutive plenary sessions were held, permitting all participants to attend each presentation. Papers on homarid and palinurid lobsters were presented in each session with additional papers on crabs, *Nephrops*, and crayfish in certain sessions. Several papers provided state-of-the-art reviews, others covered scientific findings from field and from laboratory studies, and others included new methodology or theoretical models. Individual papers were discussed briefly in each session, and usually there was a general discussion of subject material at the end of each session. Several concurrent informal evening sessions were organized either to continue discussions or to introduce additional topics or concepts. The workshop was attended by 79 scientists from Australia, Bermuda, Brazil, Canada, Cuba, France, Italy, Japan, Mexico, New Zealand, Spain, South Africa, the United Kingdom, and the United States.

The objectives of each session were as follows.

*Session 1: Introduction:* welcoming address and introduction of the theme of the Workshop.

*Session 2. Lobster Fisheries and Recruitment Variability:* to review current understanding of stock–recruitment relationships and management objectives in major lobster and crab fisheries of different countries.

*Session 3. Larval Distribution Dynamics:* to examine how larval behavior and advection is influenced by physical, chemical, and biological factors.

*Session 4. Behavior and Movement:* to explore factors affecting larval settlement and substrate preference and factors influencing activity rhythms, burrowing, and migration of benthic forms.

*Session 5. Recruitment Enhancement:* to determine the usefulness and state-of-the-art of releasing lobsters into the wild from artificial cultivation and of field techniques to examine possible benefits of stocking, artificial reefs, and sanctuaries.

*Session 6. Ecology of Population Structure:* to examine what factors (predators, competition, substrate type, food, water currents, etc.) control density, size, and production of lobsters and crabs.

*Session 7. Factors Affecting Growth and Reproduction:* to examine which factors are important in influencing growth, reproduction, and recruitment.

*Session 8. Models of Stock–Recruitment Relationships:* to examine mathematical and computer models of stock–recruitment relationships and their potential use for resource management.

*Session 9. Implications of the Workshop:* On day five, the invited Session Chairmen reviewed the papers and summarized the major findings of each session. Subsequently, aspects of future research recommendations were debated by most participants.

On the day after the Workshop, about 14 scientists, mostly from abroad, participated in a field trip on a lobster boat in Passamaquoddy Bay to experience local trap fishing for *Homarus americanus* and methods for storing lobsters in pounds.

The Workshop was successful, judging by the lively exchange of ideas, the nearly continuous discussions in and outside the main meeting room, the number of questions generated by each paper and the enthusiasm of the participants. The Workshop should have a significant impact on lobster recruitment research orientation for a number of years.

Of the 56 scientific manuscripts submitted, 48 were accepted by the Session Chairmen for the review process on the basis of completeness and general relevance to recruitment. The proceedings published in this issue contain the 34 papers that passed the standard peer review and editorial processes of the *Canadian Journal of Fisheries and Aquatic Sciences*. These papers appear in the order they were presented at the Workshop. The proceedings also include the Session Chairmen's summaries which are based on all the papers presented at the Workshop. Therefore, a complete list of all papers and posters presented and the names and addresses of participants are included in the proceedings.

Financial support for the Workshop was provided by the Fisheries Research Branch and the Scientific Information and Publications Branch of the Department of Fisheries and Oceans, Government of Canada. The Program Planning Committee consisted of D. E. Aiken, A. Campbell (Chairman), R. W. Elner, I. Pohle (Coordinator), and J. D. Pringle. D. W. McLeese was invited to be Special Editor of the proceedings. J. E. Stewart delivered the Introductory Address. The Session Chairmen were D. E. Aiken, J. S. Cobb, G. Y. Conan, M. J. Fogarty, W. F. Herrnkind, B. F. Phillips, and J. D. Pringle. J. F. Caddy co-chaired Session 9 with A. Campbell to obtain the concluding summary remarks. The many individuals who contributed their time and helped in various ways to make the Workshop a success include E. M. Campbell, F. Cunningham, D. R. Duggan, B. J.Fawkes, G. E. Fawkes, D. E. Graham, S. L. Hamet, J. Hurley, B. Lawrence, P. Lawton, J. Matthews, W. McMullon, I. A. Milewski, G. Pohle, S. Polar, D. A. Robichaud, D. M. Tremblay, A. Williamson, and W. Young-Lai.

## References

PHILLIPS, B. F., AND J. S. COBB. 1977. Workshop on lobster and rock lobster ecology and physiology. CSIRO Dir. Fish. Oceanogr. (Aust.) No. 7.

# Session 1
# Introduction

# Introductory Address

James E. Stewart

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The International Workshop on lobsters held in 1977 in Perth, Western Australia, was a signal success and led to the two-volume review "The Biology and Management of Lobsters" edited by Cobb and Phillips (1980). This excellent work contained a quote from Munro (1974), who, in speaking of lobster fisheries, said: "few of the biological and ecological details necessary for rational management are available. However, this has not prevented the imposition of quotas, closed seasons, minimum size limits, prohibition of fishing gear, or restrictions on the capture of berried females in many areas. Some of the measures have been of rather dubious value, while others appear to have needlessly restricted development of the fisheries." Unfortunately, 11 yr later, the management of most lobster fisheries has changed little.

Since lobsters form the basis of economically valuable fisheries around the world and are characterized often by declining stocks, it behooves us to move quickly to define that information required to provide adequate management regimes, and to institute the necessary research programs to collect and interpret this information. The 1977 Workshop in Australia aided this process greatly and has provided considerable focus and impetus for both defining and implementing the appropriate studies. One of these areas clearly is recruitment, which was defined in the broadest sense by the conveners of the present Workshop as "the number of progeny derived from a spawning population surviving to a subsequent life stage." In commercial terms this means the number surviving to marketable sizes. The areas of concern include, among other things, (1) location and size of brood stock, (2) larval distribution in relation to oceanographic phenomena, (3) location and magnitude of larval settlement, (4) behavioral and population ecology of juveniles, (5) food preferences, requirements, and availability, (6) growth rates, and (7) stock identity and migration.

Whether such information can be collected in sufficient detail to be useful for real time predictions is both a challenge and a moot point. Regardless, clear understanding of these and other factors would permit management regimes to be based upon scientific principles rather than upon arbitrary and empirically based judgements, and would meet part of Munro's plea for rational management.

Recruitment, as defined for the purposes of this Workshop, brings attention to bear rather broadly, but also in depth, on the biology and ecology of the lobsters before their entry into the fisheries. Prior to the last 10 yr, most of the fisheries research was concentrated on the lobster after it had entered the fishery, thus treating it in effect as a short-lived species. Thus, despite fairly extensive and intensive studies over the past 100 yr on clawed lobsters, we are still lacking detailed and quantitative information on the life history and behavior of lobsters in the natural environment for the periods prior to their entry into the fisheries. This Workshop, concentrating as it does on recruitment, is the appropriate format in which to attempt to resolve questions in this critical area of lobster biology.

It is also appropriate for this Workshop to be held in St. Andrews, New Brunswick. Much of the Canadian research on lobsters and fisheries generally (groundfish, scallops, crab, etc.) began here. In addition, the lobster fishery is particularly important on the Canadian Atlantic coast, it is second in value only (around $200 million market value) to the large cod fishery, and employs 10 148 fishermen throughout the Atlantic Zone.

Following the early work of Knight, in-depth lobster research work began at St. Andrews with scientists such as W. Templeman, D. G. Wilder, and D. W. McLeese in the 1930's, 1940's, and 1950's extending the pioneering work of Herrick (1909). Canadian lobster studies are now more broadly based; the numbers of scientists involved are greater, as you will see as the Workshop progresses. Studies on the lobster *Homarus americanus* are now also being carried out at centers in St. John's, Newfoundland, Halifax, Nova Scotia, Moncton, New Brunswick, Prince Edward Island, and Quebec. Work at these centers covers physiology, behavior, nutrition, pollution, toxicology, and disease, as well as general biology and ecology. It is our belief that, through study of the full range of life sciences, we will develop an in-depth and comprehensive picture of this valuable and interesting animal.

Given this and my history, I would be remiss if I did not at least mention, if not attempt to persuade you, of the importance of disease as a critical influence on species abundance at different life history stages. Many scientists consider disease to be one of the key factors limiting population size. A number of examples exist where specific diseases have either periodically reduced the population or virtually eliminated it.

Aquatic examples are (1) Malpeque disease of the oyster, *Crassostrea virginica*, (2) parasitic castration of blue crabs, *Callinectes sapidus*, (3) crayfish plague in Europe affecting the genus *Astacus*, (4) Fungal disease of herring caused by *Ichthyophonus hoferi*, (5) amoeboid disease of the green sea urchin, *Strongylocentratus droebachiensis*, and (6) gaffkemia, the bacterial disease of lobsters (genus *Homarus*), the characteristics of which are as follows: all age groups from early benthic to mature adults are susceptible; the infections are fatal but temperature dependent; a highly specific pathogen, *Aerococcus viridans* (var.) *homari*, is involved; the pathogen enters the blood system through wounds or breaks in the integument; on occasion, the infections have a high prevalence, leading to major epidemics in holding units; no studies have been conducted to determine lobster mortalities in the wild, but we anticipate that the disease has considerable effect on feral stocks, since the prevalence of infections in the wild are often high.

Finally, on behalf of the Fisheries Research Branch, Atlantic Fisheries Service, I welcome you to St. Andrews and wish you every success in resolving the most important factors governing recruitment for the different species of lobsters and crabs and how this information can be applied or used to develop rational

management measures.

Again, a welcome to old friends and new who have come from so many countries to accomplish this task.

## References


COBB, J. S., AND B. F. PHILLIPS. [ED.]. 1980. The biology and management of lobsters. Vol. I and II. Academic Press, New York, NY.

HERRICK, F. H. 1909. Natural history of the American lobster. Bull. U.S. Bur. Fish. 29: 149–408.

MUNRO, J. L. 1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Scientific report of the ODA/UNI fisheries ecology research project, 1962–73. Part VI. The biology, ecology and bionomics of Caribbean reef fishes — Crustaceans (spiny lobsters and crabs). Univ. West Indies Zool. Dep. Res. Rep. 3: 1–57.

*(Photograph courtesy of Dr. Phyllis Johnson)*

# Dr. Martin W. Johnson

The Proceedings of the International Workshop on Lobster Recruitment are dedicated to the late Dr. Martin W. Johnson. His studies on the systematics and ecology of certain eastern Pacific lobster larvae, and in particular the California spiny lobster (see both Pringle and Phillips, this volume), are seminal works. He was the first to suggest the importance of physical oceanic phenomenon as lobster larval retainers within the dynamic California Current.

To make our choice of the late Dr. Johnson even more appropriate, he was replete with Canadian connections: when he was a boy, his parents homesteaded in Saskatchewan; during the early 1930's he served on the Passamaquoddy International Fisheries Commission, which frequently brought him to the St. Andrews Biological Station; and his daughter, Dr. Phyllis Johnson, studied with Dr. James E. Stewart at the Halifax Fisheries Research Laboratory.

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# Session 2
# Lobster Fisheries and Recruitment Variability

Chairman: J. D. Pringle

*Department of Fisheries and Oceans, Fisheries Research Branch, Scotia–Fundy Region, Invertebrates and Marine Plants Division, Halifax Fisheries Research Laboratory, P.O. Box 550, Halifax, N.S. B3J 2S7*

# Stock Definition, Recruitment Variability, and Larval Recruitment Processes in the American Lobster, *Homarus americanus*: A Review

G. P. Ennis

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Ennis, G. P. 1986. Stock definition, recruitment variability, and larval recruitment processes in the American lobster, *Homarus americanus*: a review. Can. J. Fish. Aquat. Sci. 43: 2072–2084.

A review of the literature pertaining to stock definition, causes of variability in recruitment to standing stocks, and larval recruitment processes in the American lobster, *Homarus americanus*, is presented. Several stocks can be identified but their boundaries are indistinct. The areas are too large for consideration of any of the stocks as a single management unit. The bulk of annual landings is composed of recruitment to standing stocks since the preceding fishing season. Landings for all areas fluctuate and there is considerable variability in patterns of fluctuations between areas. Suggested causes of variability in recruitment include variation in temperature, variation in annual river discharge, fishery induced variability in egg production, man-made interruption in larval supply, and ecosystem change. Mechanisms that determine where larvae that originate in a given area eventually settle are uncertain. Literature on larval recruitment processes contains theories based on passive transport of larvae by surface currents and others based on interacting behavioral and hydrographic mechanisms that may enable larvae to maintain position near parental grounds.

L'article présente un examen des publications concernant la définition des stocks, les causes de variabilité du recrutement dans les stocks exploitables et les processus de recrutement des larves du homard américain, *Homarus americanus*. Il est possible de repérer plusieurs stocks, mais leurs limites sont indistinctes. Les régions sont trop vastes pour qu'on puisse considérer aucun des stocks comme une seule unité de gestion. La plus grande partie des débarquements annuels se compose du recrutement dans les stocks exploitables par rapport à la saison de pêche précédente. Dans toutes les régions, les débarquements fluctuent, et on relève une variabilité considérable d'une région à l'autre. La variabilité du recrutement peut s'expliquer par des variations de la température et de l'écoulement annuel d'eau douce, par la variabilité de la production d'œufs causée par la pêche, par l'interruption de l'approvisionnement en larves due à l'homme et par des modifications de l'écosystème. Les mécanismes qui déterminent où s'installent les larves produites dans une région donnée sont mal connus. Les publications sur les processus de recrutement des larves présentent des théories fondées sur le transport passif des larves par les courants superficiels et d'autres basées sur l'interaction de mécanismes comportementaux et hydrographiques qui peuvent permettre aux larves de rester à proximité de la zone où se trouvent leurs géniteurs.

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Knowledge of the relationship between stock size and subsequent recruitment to the stock is important in order to effectively manage a fishery. Requirements for determination of a stock–recruitment relationship include (1) a population that is more or less discrete both geographically and biologically (i.e. a stock), (2) a measure of stock size over a period when abundance ranged widely, (3) a measure of subsequent recruitment to the stock which coincides with the same time period, (4) an understanding of the effect of variation in factors other than stock size on recruitment variability, and (5) an understanding of recruitment processes for the stock. The foregoing has not been achieved for any population of the American lobster, *Homarus americanus*. Fisheries on this species are characterized by high exploitation rates and minimum legal sizes at or below the smallest sizes at which females mature. With this general situation, widespread recruitment failure is considered to be a distinct possibility (Anonymous 1977, 1979). This makes an understanding of stock and recruitment for consideration in the fisheries management process vitally important.

This paper reviews and summarizes the literature relevant to stock and recruitment in the American lobster.

## Definition of American Lobster Stocks

A definition of the term "stock" acceptable to everyone with an interest in intraspecific groupings may be unattainable. Perceptions may range from a genetically discrete subunit of a species to no more than geographical boundaries based on practical resource management rather than biological considerations. In practice, some compromise between biological and management considerations is usually the case (see Booke 1981; Ihssen et al. 1981; MacLean and Evans 1981 for reviews). In this consideration of stock separation in the Ameri-

can lobster, no particular definition of stock is followed and the term is used loosely. However, Ihssen's et al. (1981) definition as "an intraspecific group of randomly mating individuals with temporal or spatial integrity" is provided for reference.

The American lobster ranges from southern Labrador to north Carolina (Cooper and Uzmann 1980) (Fig. 1). There are intensive fisheries on coastal populations throughout its range with official landings statistics dating from the early 1870's for some areas. Offshore populations occur along the outer edge of the Continental Shelf and upper slope (at depths of about 110–450 m) from the southern Scotian Shelf off Nova Scotia southwards to Virginia (Cooper and Uzmann 1980). Offshore fisheries started in about 1955 and are not as intensive as those inshore.

## Tagging

Tagging studies have demonstrated that in coastal areas, lobsters are nonmigratory although some individuals move considerable distances (Wilder 1963; Morrissey 1971; Dow 1974; Fogarty et al. 1980). Although this should promote establishment of reproductively isolated population units, the more or less continuous distribution of lobsters in coastal areas makes separation of the units difficult.

Offshore lobsters, on the other hand, are migratory. It has been estimated that at least 20% of the offshore population from eastern Georges Bank southward migrate into shoal water during spring and summer, where some mixing with the inshore population occurs, and then move offshore by late fall (Uzmann et al. 1977). Among the offshore lobsters, there is also considerable movement along the outer edge of the Continental Shelf (Uzmann et al. 1977). Tagging indicates that lobsters in this offshore area are discrete from those in coastal areas and that within this area there appear to be no distinct populations. In contrast, however, there is evidence from tagging of interchange between coastal lobsters of southwestern Nova Scotia and those offshore on the southern Scotian Shelf (Campbell and Stasko 1985). Recent tagging studies indicate extensive mixing of offshore lobsters from southern Scotian Shelf, deepwater areas of the Gulf of Maine – Bay of Fundy, and Georges Bank. Seasonal inshore–offshore migrations result in considerable mixing of coastal and offshore lobsters throughout this area (Campbell 1986; Campbell and Stasko 1986), which indicates that these lobsters are not discrete.

## Morphometrics

Based on multivariate analyses of morphometric data, Saila and Flowers (1969) concluded that there are differences between inshore and offshore lobsters. Their samples from different inshore localities (which include Boothbay, Boothbay Harbor, and Casco Bay, Maine; Rhode Island; Massachusetts; Long Island; and Connecticut) and from different offshore localities (which include Veatch and Hudson canyons) were not adequate for detailed comparisons, but there were indications of differences within both the inshore and offshore areas. They acknowledged that the nature (phenotypic or genotypic) of the observed difference between inshore and offshore lobsters remained to be resolved by other techniques; however, they suggested that morphometric differences are of adaptive significance and therefore probably reflect genetic differences. Similarly, Rogers et al. (1968) found that stage I larvae collected offshore near the edge of the Continental Shelf and presumably spawned in that area were significantly larger than stage I larvae taken close inshore in southern New England. This contrast in size was not found in later larval stages. These authors could only speculate whether the differences were of genetic origin or reflected such influences as the size of the brood lobsters, the size of the eggs, or other environmental factors.

## Electrophoresis

Barlow and Ridgway (1971) demonstrated the potential for examination of genetic variation between lobster populations using electrophoretic techniques. However, at a single locus (position on chromosome) they found no indication of genetic variation between lobsters collected near Boothbay Harbor and lobsters collected along the edge of the Continental Shelf between Hudson and Lydonia canyons. Also using electrophoretic techniques, Tracey et al. (1975) found low levels of genetic variability at 44 loci among lobsters from three offshore areas (a mixed sample from Lydonia, Welker, and Hydrographer canyons; Continental Shelf between Hudson and Block canyons; and at the mouth of Hudson Canyon) and among lobsters from five inshore areas (southern Gulf of St. Lawrence; Bay of Fundy; Boothbay Harbor; Woods Hole and Martha's Vineyard, Massachusetts). Differentiation was found only at a single locus (i.e. malic enzyme *Me*). In the two Massachusetts inshore areas almost all individuals were homozygous for the $Me^{100}$ allele whereas in the southern Gulf of St. Lawrence sample the $Me^{100/100}$ genotype was absent and almost all individuals were homozygous for the $Me^{102}$ allele. Among individuals taken offshore between Hudson and Block canyons and in Lydonia, Welker, and Hydrographer canyons, 25% were $Me^{100/100}$, 25% $Me^{102/102}$, and 50% heterozygous $Me^{100/102}$. These genetic differences indicate an absence of gene flow between the Gulf of St. Lawrence and Massachusetts inshore populations. The divergence of allelic frequencies also suggests strong populational differentiation between these inshore and the offshore populations (Tracey et al. 1975). In samples collected inshore at southwestern Nova Scotia and some 130 km offshore on the southern Scotian Shelf, Odense and Annand (1978) found no significant genetic differences using electrophoretic techniques. This is another indication that inshore and offshore lobsters in this area are not discrete.

Electrophoretic studies indicate relatively low levels of genetic variability between American lobster populations. Only for widely separated populations (such as southern Gulf of St. Lawrence and Massachusetts inshore areas) are the genetic differences sufficiently great to indicate an absence of gene flow between them.

## Fishery Trends

Campbell and Mohn (1983) used principal-component and cluster analyses of historical landing data from Maine and most of Atlantic Canada as a basis for defining lobster stocks. Their analyses suggest at least three general stocks: (1) Maine, the Bay of Fundy, inshore and possibly offshore southwestern Nova Scotia; (2) the eastern coast of Nova Scotia (from Queens to Richmond counties); and (3) the Gulf of St. Lawrence, which was subdivided into six areas. Except for central Northumberland Strait, however, these areas were closely related in landing trends which precludes their consideration, based on these analyses, as separate stocks within the Gulf of St. Lawrence.

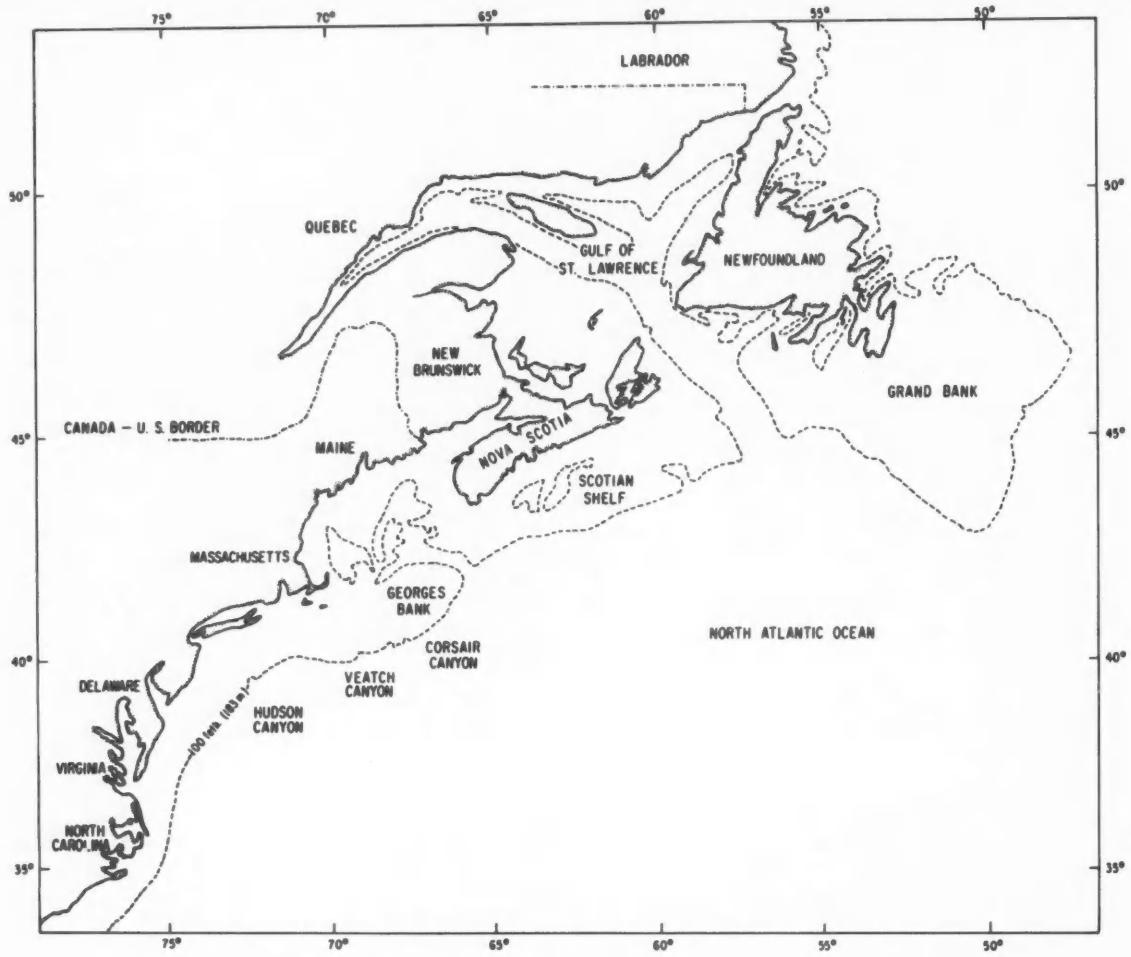


FIG. 1. Eastern North America encompassing the range of the American lobster, *Homarus americanus*.

## Population Parameters

Significant differences in some aspects of lobster population biology have been noted between areas. Templeman (1935) described changes (increases) in relative size of claws in males, relative abdomen width in females, and weight of males compared with females in relation to size, all of which are associated with onset of sexual maturity. In southern Gulf of St. Lawrence lobsters, sexual maturity, and hence these changes, occurs at much smaller sizes than in Bay of Fundy lobsters, with those of the eastern coast of Nova Scotia being transitional (Templeman 1935, 1936a, 1944; Campbell and Robinson 1983).

Growth rate varies widely throughout the range of the species. Russell (1980) presented eight growth curves for various United States inshore populations which form a wide band on the same graph. Lengths-at-age derived from von Bertalanffy parameters presented by Russell (1980) and Cooper and Uzmann (1980) for United States offshore lobsters generally fall above this band. Lengths-at-age for Bay of Fundy lobsters (Campbell 1983) fall in the upper region of the band of growth curves for United States inshore lobsters, and those for Newfoundland lobsters (Ennis 1980; Ennis et al. 1982) fall below. Although southern Gulf of St. Lawrence lobsters generally are considered to be fast growing, the only estimates of length-at-age that are available were generated by Wilder (1953), and they suggest a growth curve in the lower region of the band.

The wide variation in size at maturity and growth rate throughout the range of the American lobster is probably more a reflection of physiological responses to different environmental and ecological conditions than a reflection of genetic variation. Such phenotypic variation, however, is useful in stock separation (Ihssen et al. 1981). In comparing population parameters of lobsters from different areas, one must consider the impact on population dynamics of the fishery management regime in each area. In any population, for example, a different dynamic response to exploitation will likely result if the minimum legal size is set at 81 mm carapace length (CL) and the exploitation rate at 60% than if these management controls are set at 65 mm and 90%.

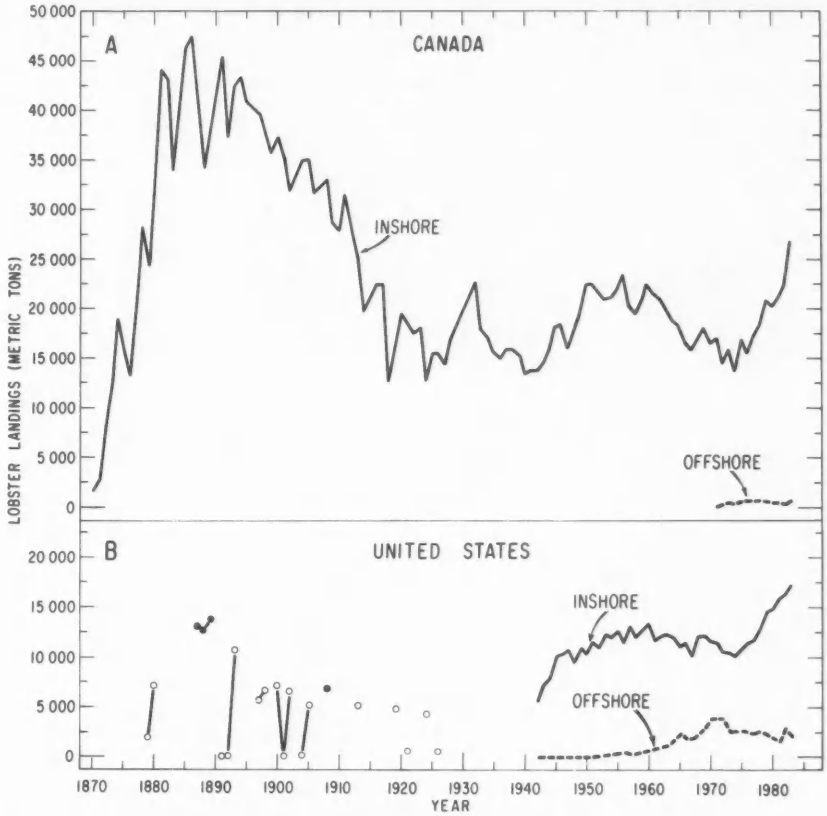


FIG. 2. Historical landings of the American lobster, *Homarus americanus*, in (A) Canada and (B) the United States. Open points in Fig. 2B indicate incomplete data for those years.

### Stocks Versus Management Units

The evidence demonstrates that the American lobster is divided into a number of different stocks. These stocks occur over broad geographical areas between which it is not presently possible to define precise boundaries.

The number of lobster resource management units greatly exceeds the number of definable stocks. The Atlantic coast of Canada is divided into 20 lobster management districts (Anonymous 1975) and in the United States lobsters are fished in 11 states, each with responsibility for management (Anonymous 1978). The offshore lobster fisheries in Canada and in the United States are managed separately from the inshore fisheries. The Canadian offshore fishery is relatively small and operates out of southern Nova Scotia. In the United States, most of the 11 states with an inshore fishery also fish offshore.

The southern Gulf of St. Lawrence and the eastern coast of Nova Scotia, which are considered separate stock areas (Robinson 1979; Campbell and Mohn 1983; Campbell and Robinson 1983), have five districts each. District 4B extends along the east and south coasts of Nova Scotia and overlaps what is considered two stock areas. A number of districts overlap two, and in one case three, provincial boundaries. Even within existing management districts, the problems and considerations with which managers have to deal can be so varied from area to area as to preclude implementation of any management measure that will be effective, equitable, and applicable throughout the district. This realization resulted in the number of lobster management districts in Newfoundland being increased from 4 to 12 (Ennis 1982).

Ineffective management in one area could have repercussions in others. It is important that the consequences of varying management regimes within difference areas of a stock be known and considered by managers in order that overall conservation requirements of the stock can be met. For the American lobster, this will require a clearer definition of stocks than is presently available.

## Variability in Recruitment to Standing Stocks

The fishery for the American lobster did not assume major commercial importance until after 1840 (Dow 1980). Historical landing data indicate a very rapid development of the fishery during the late 1800's both in Canada and the United States (Fig. 2). Annual landings peaked at around 60 000 t (Canada and the United States combined) between 1880 and 1890 and then dropped to around 20 000 t during the 1920's. Subsequently, landings have fluctuated but at generally higher levels than during the 1920's. In recent years, landings have

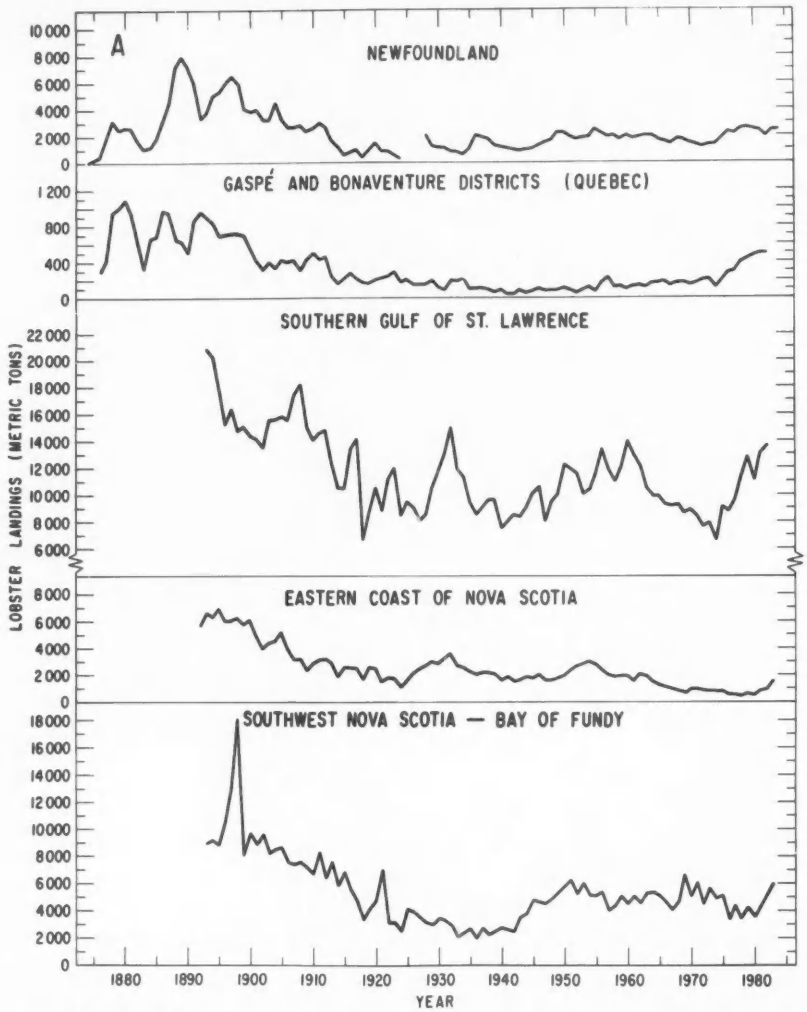


FIG. 3. Historical landings of the American lobster, *Homarus americanus*, in several inshore fishing areas of (A) Canada and the (B) United States. Open points in Fig. 3B indicate incomplete data for those years.

increased fairly steadily and significantly from around 30 000 t annually during the early 1970's to 47 000 t in 1983 (Fig. 2).

Exploitation rates in most inshore lobster fisheries generally are in excess of 80–85% annually and appear to have been high for many years (Anthony 1980; Campbell 1980). Therefore, recruitment to the standing stock (or the commercially legal portion of the population), through growth into the commercial size range, of lobsters that are smaller than the minimum legal size is the source of the bulk of the landings. It follows that for much of the history of the fishery, annual landings are a good indicator of recruitment to standing stocks for that year (Ennis et al. 1982; Ennis 1983a; Campbell and Mohn 1983).

Annual landings for major regions covering most of the species' geographic distribution demonstrate marked fluctuations and considerable variability in patterns of fluctuations in landings between areas (Fig. 3). Lobster landing data are available for relatively small statistical reporting units throughout Atlantic Canada. Neighboring statistical units can have similar or different fluctuations in annual landings, and patterns for individual units can be quite different from patterns for lobster districts or other large statistical areas of which they are part (Anonymous 1975; Iles 1975; Stasko 1980a; Campbell and Mohn 1983).

Suggested causes of or contributors to fluctuations in recruitment to standing stocks of lobsters in different areas include (1) temperature variation, (2) variation in annual river discharge, (3) fishery-induced variability in egg production, (4) man-made interruption in larval supply, and (5) ecosystem changes. Each of these is considered below.

## Temperature

Dow (1969) demonstrated a close association between cyclic variation in mean annual sea surface temperature (representing

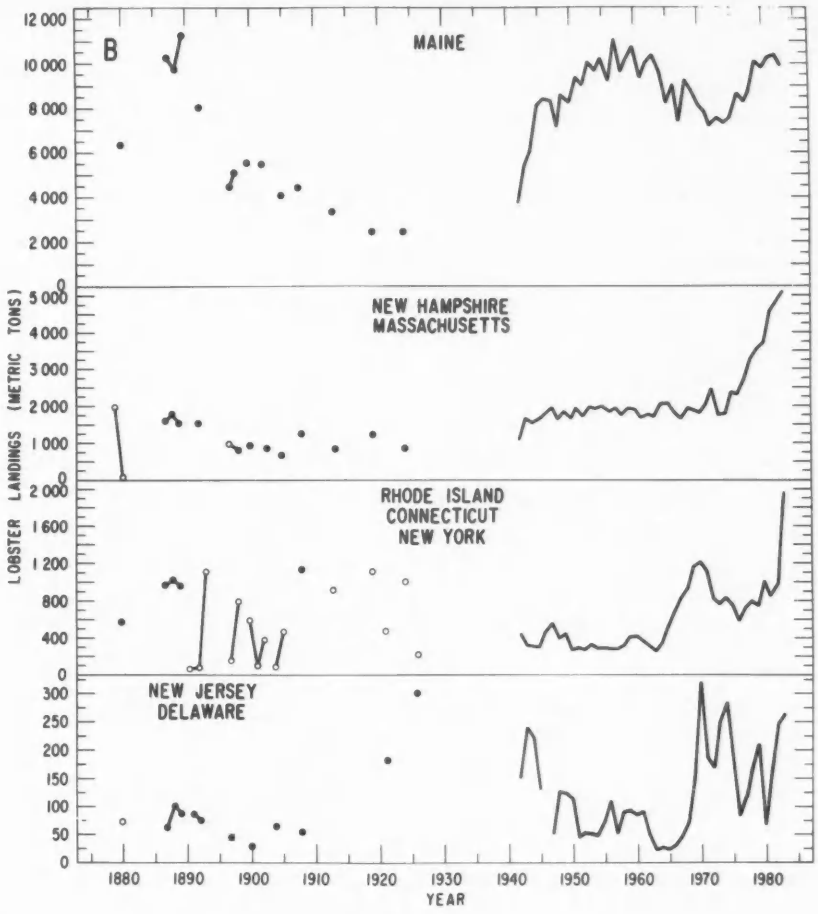


FIG. 3. (*Concluded*)

general climatic trends) at Boothbay Harbor and lobster landings throughout most of its range. During a warming trend over 1939–53 followed by a cooling trend over 1953–67, he noted record high landings for different areas occurring sequentially from south to north then from north to south. This he suggested was related to the northward and southward drift of "optimum" (9.2–10.7°C, mean annual) temperatures.

In a stepwise multiple regression performed on mean annual sea surface temperature at Boothbay Harbor and Maine lobster landings for 1940–70, Flowers and Saila (1972) found that temperature of the same year as the landings was significant but second in importance to the lagged temperature combination of 6, 7, and 8 yr previous. Mean annual temperature 6 yr previous to the year of landings was the most significant contributor. Low winter (January through March) temperatures were found to be more significant than high summer temperatures. For temperature 6, 7, and 8 yr previous, this may indicate high first year (0+ juvenile) mortality during colder winters. For temperature of the same year, it may indicate less recruitment to the standing stock because of lower molting frequency among sublegal size lobsters and possibly also reduced catchability in the fishery due to lower temperature (Flowers and Saila 1972). Their analyses of 1951–69 temperature and landing data for Nova Scotia revealed that temperature of the previous year could be an indicator of landings, the reason being that the Nova Scotia fishery is primarily a spring fishery ending around the last of June and heavily dependent on recruitment which takes place the summer previous to the fishery (Flowers and Saila 1972).

Follow-up studies by Dow (1977, 1978) demonstrated significant correlations between mean annual temperature at Boothbay Harbor and mean lobster landings for Maine of 4–7 yr later and between total inshore landings and mean annual temperature at Boothbay Harbor 6 and 7 yr earlier. Sophisticated empirical models also have been used to analyze various time series of lobster landing – temperature data. These analyses confirm the relationship between temperature and lobster landings and the importance of the time lag between the two (Boudreault et al. 1977; Orach-Meza and Saila 1978; Fogarty 1984).

In his analysis of data from lobster larval surveys conducted in Northumberland Strait (southern Gulf of St. Lawrence) from 1948 to 1961, Scarratt (1964) found that larval survival varied from year to year but did not appear to be related to surface

temperature. Caddy (1979), however, reanalyzed the data and concluded that temperature during the larval period had a major influence on larval survival. He found that the temperature sum required for successful completion of the four larval stages increased with declining ambient temperature. This limits the period when hatching can result in production of stage IV larvae within a reasonable time. This limitation is particularly serious for the later stages which require higher ambient temperature to complete development. It was postulated that at low temperatures, molting from stage IV to V may be delayed indefinitely (Caddy 1979). His analyses demonstrated higher survival rates for larvae hatched early in the season than for those hatched later.

Variability in temperature conditions is an important factor influencing recruitment to standing stocks of lobsters. Temperature acts primarily by affecting growth rates of larvae, juveniles, and adults. Larval survival appears to be greatly affected by changes in the time required to complete development. Survival to recruitment is also affected by changes in the time required for newly settled juveniles to reach recruitment size as a result of changes in growth rate. The number of lobsters of a particular year-class that eventually recruit to a standing stock is influenced by temperature to a large extent.

### Freshwater Runoff

Sutcliffe (1972) presented evidence of a positive correlation between St. Lawrence River discharge and canned lobster production in the province of Quebec. A 6-yr lag (approximating age at recruitment to the standing stock) was required to match catch and runoff, indicating that runoff is perhaps affecting larval survival or growth. Subsequently, he reported no correlation between annual abundance of lobster larvae in Northumberland Strait (from Scarratt 1964, 1973) and St. Lawrence River discharge (Sutcliffe 1973). However, he obtained a correlation ($r = 0.769$, $P < 0.01$) between larval abundance and June runoff in the same year from the Miramichi River, the largest river in the general area of the larval sampling. The correlation with June runoff decreased for later larval stages. It was noted that for all four larval stages the highest correlation was with June runoff, lending support to Scarratt's (1964) thinking that larvae produced in the earlier part of the season have a better chance of survival.

In further analyses of total lobster landings for Quebec (1930–69) and St. Lawrence River discharge, a correlation ($r = 0.831$, $P < 0.001$) was obtained using April runoff and a 9-yr lag (Sutcliffe 1973). A 9-yr lag gave a better correlation than the 6-yr lag used initially (Sutcliffe 1972) because the landing data included market (≥81 mm CL) lobsters as well as the canned (smaller lobsters) production which was used in the original correlation. For the same period, Prince Edward Island lobster landings are best related to June discharge from the St. Lawrence River using an 8-yr lag ($r = 0.853$, $P < 0.001$). The shorter time lag may be explained by regulations that allow smaller lobsters to be landed in Prince Edward Island than in Quebec.

In the figure illustrating the 1939–68 Quebec lobster landings and 1930–69 St. Lawrence River discharge for April (Sutcliffe 1973), a sharp increase in river discharge from 1963 to 1969 can be seen. It was suggested that if the pattern between landings and discharge continued, a trend towards increased Quebec lobster landings should be evident by 1975. Sutcliffe's (1973) figure is included here (Fig. 4) with more recent landings and river discharge data added. The upward trend in landings between 1972 and 1978 matches the 1963–69 discharge trend as he predicted. Sheldon et al. (1982) developed Sutcliffe's (1973) relationship between Quebec lobster landings and river runoff into a predictive model. A multiple regression that explained 77% of the variation provided an apparently reliable basis for forecasting landings.

Bugden et al. (1982) provided a detailed consideration of the mechanisms through which freshwater runoff may influence biological production generally and particularly production of commercially utilized species in the Gulf of St. Lawrence. Among the factors affected by runoff variability are water circulation, water mixing patterns and intensity of mixing, ice formation and distribution, heat retention (temperature near surface), direct nutrient enrichment, salinity, turbidity, light penetration, and intensity of stratification. These factors directly affect primary production and, as a result, plankton dynamics generally. Obviously, the mechanisms through which runoff affects biological production in the sea involve complex interactions between various physical, chemical, and biological processes.

For many fish stocks, it has been concluded that year-class strength is determined during the larval phase (Bugden et al. 1982). If so, it is logical to conclude that if freshwater runoff variability has a major influence on plankton dynamics and/or the physical oceanographic characteristics of the larval environment, such effects should influence year-class strength (Bugden et al. 1982).

### Fishery-Induced Variability in Egg Production

A minimum legal size has been a management tool in fisheries for the American lobster from early years. Present size limits, in effect for many years, range from $2\frac{1}{2}$ in. (63.5 mm) to $3\frac{3}{16}$ in. (81 mm) CL. In many cases, size limits are near and even below the size at which most female lobsters lay eggs. For example, in the southern Gulf of St. Lawrence the minimum legal size is 63.5 mm CL and the smallest egg-bearing females there are about 60 mm CL. In the Bay of Fundy and southwestern Nova Scotia the minimum legal size is 81 mm CL and the smallest egg-bearing females occur at 85 mm CL (Robinson 1979; Campbell and Robinson 1983). Considering the high exploitation rates that prevail in most areas, it is obvious that egg production is generally very low and could limit recruitment. Low levels of egg production are such a common feature of lobster fisheries that ICES *Homarus* Working Groups (Anonymous 1977, 1979) raised the possibility of widespread recruitment failure if current management regimes continue.

All fisheries for the American lobster also have a regulation prohibiting retention of egg-bearing females. This likely provides substantial protection to the limited egg production that does occur. Variability in compliance with the regulation could result in some variability in annual egg production in an area, but this would likely be small.

In two major Canadian lobster fishing areas, landings declined to such low levels during the 1970's that the fisheries were considered to be collapsed. By 1980, landings in central Northumberland Strait and along eastern Nova Scotia were less than 10% of those during the early 1900's (Campbell and Robinson 1983; Campbell and Mohn 1983). Peak landings exceeded 5443 t during the early years of the fishery in central

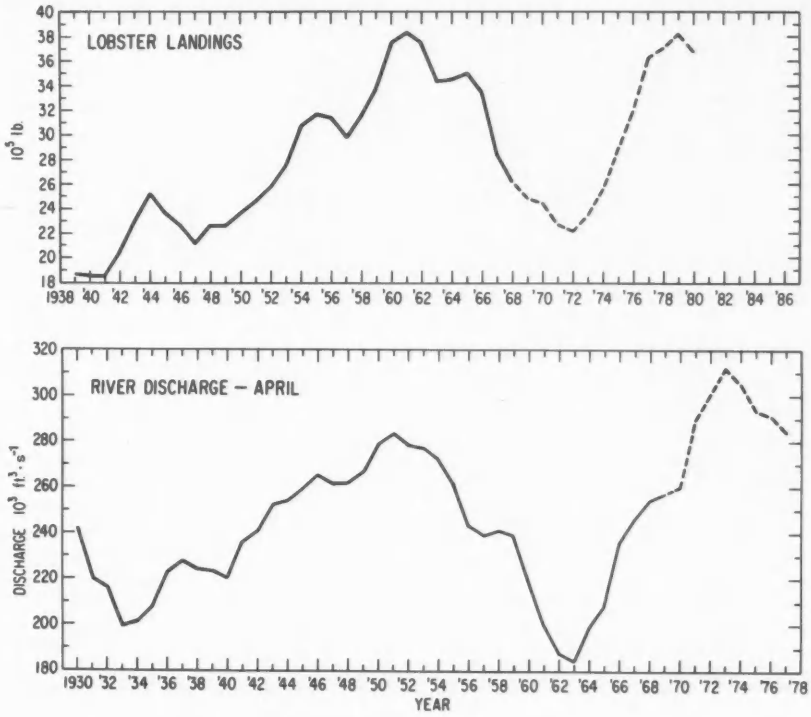


FIG. 4. Annual Quebec lobster landings and St. Lawrence River discharge for April (3-yr running averages and a 9-yr lag). (From Sutcliffe (1973) with data beyond 1969 added)

Northumberland Strait but in 1974 dropped to about 454 t, the lowest level on record (Fig. 3A). Similarly, along eastern Nova Scotia, landings peaked at over 6804 t during the early years of the fishery but dropped to less than 907 t in 1977 (Fig. 3A). On the basis of a comprehensive review of the available historical information for each of these fisheries, along with a detailed consideration of the biology of lobsters in each area, Robinson (1979) concluded that recruitment failure due to inadequate egg production was the cause of collapse in both cases. This conclusion was supported by Stasko (1980a) in the case of central Northumberland Strait and by biologists responsible for generating management advice on lobster resources in Atlantic Canada in the case of eastern Nova Scotia (McCracken 1979).

Fishery collapse in these areas led to reduced effort during the 1970's. At least for eastern Nova Scotia it is considered likely that the reduced effort resulted in reduced exploitation rates (Pringle and Duggan 1984), and it has been suggested that the slight recovery that has occurred in that fishery recently (Fig. 3A) is related to increased egg production (Pringle and Duggan 1984). Increased landings, however, are likely to encourage increased effort, and it is anticipated that the recent improvement in landings will not be maintained (Pringle and Duggan 1984).

## Man-Made Interruption in Larval Supply

Completion of the Canso Causeway in 1954, connecting mainland Nova Scotia with Cape Breton Island, blocked the flow of water through Canso Strait (see Fig. 5). Dadswell (1979) hypothesized that lobster larvae originating in the southern Gulf of St. Lawrence and transported through the Canso Strait had been an important source of recruitment for populations in Chedabucto Bay on the Atlantic coast of Nova Scotia. He attributed the lobster fishery collapse along eastern Nova Scotia during the 1970's to recruitment failure caused by closure of Canso Strait. His basic premise was that lobster larvae are transported downstream by surface currents so that recruitment to a population originates some distance upstream. Based on analysis of landing trends along eastern Nova Scotia, Dadswell (1979) concluded that the Canso Causeway eliminated the supply of larvae from the southern Gulf of St. Lawrence to Chedabucto Bay. This led to fishery collapse and reduced larval production in that area. Because there is a southwesterly flowing residual current along the eastern Nova Scotia coast, Dadswell (1979) suggested that reduced larval production in the Chedabucto Bay area led to recruitment failure sometime later in downstream areas.

Using the same premise regarding larval transport as Dadswell (1979), Harding et al. (1983) estimated that larvae originating in the southern Gulf and transported through Canso Strait prior to construction of the causeway contributed as much as 60% of the average landings in Chedabucto Bay during the 11 best yr of this fishery. They attribute recruitment failure along eastern Nova Scotia to the synchronous closure of Canso Strait and the start of a general climatic cooling in which a critical low temperature may have been reached at which larval

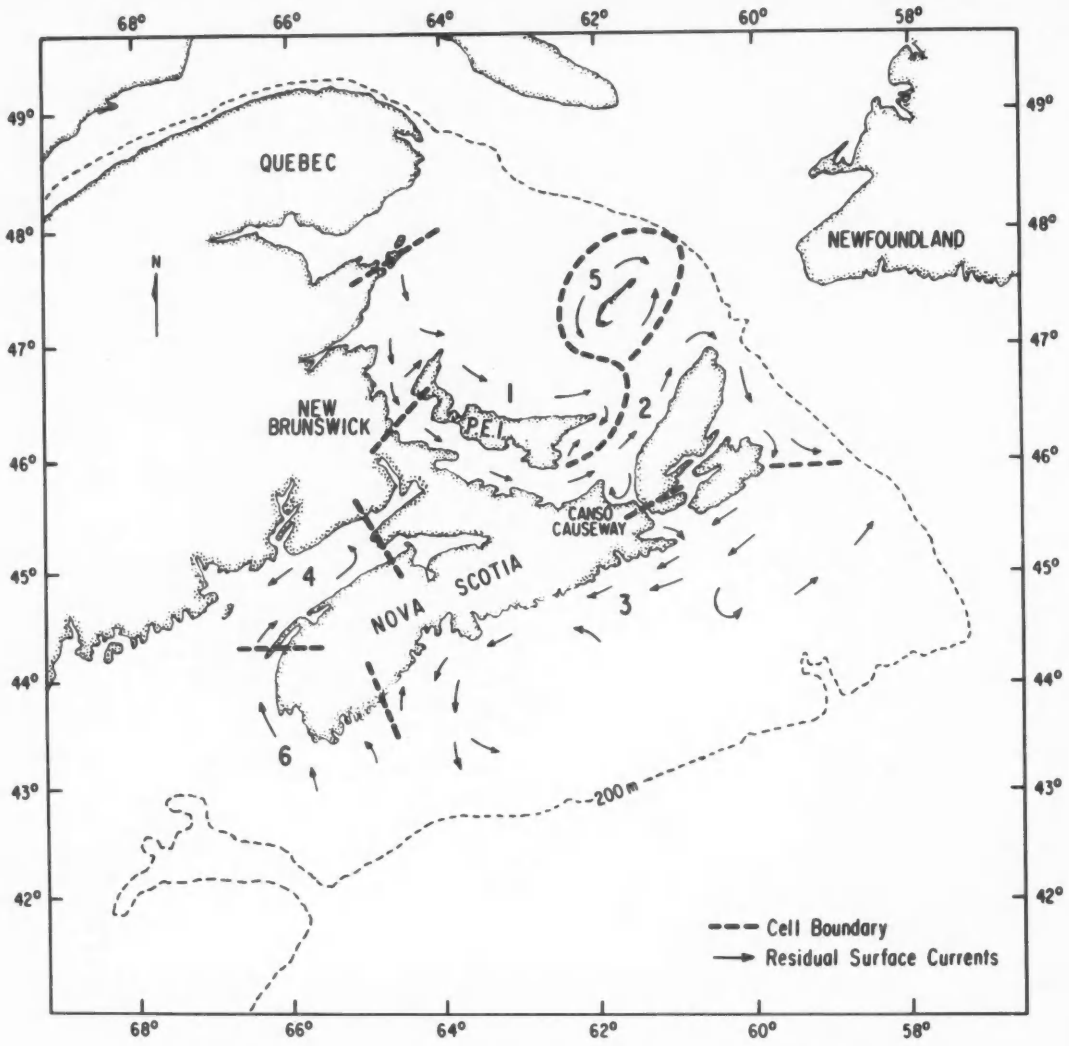


FIG. 5. Six American lobster, *Homarus americanus*, recruitment cells in the Canadian Maritimes as proposed by Dadswell (1979).

survival was much reduced.

Evidence is considered later in this paper which indicates that lobster larvae are not passive surface current drifters as Dadswell (1979) and Harding et al. (1983) assumed. Their conclusions regarding the closure of Canso Strait being the cause of recruitment failure in the lobster fishery along eastern Nova Scotia are likely not valid. However, construction projects such as the causeway across Canso Strait undoubtedly change water circulation patterns in localized areas. Such changes are usually permanent; therefore, their influence on variability in recruitment to standing stocks of lobsters would be limited to pre- and post-construction conditions.

## Ecosystem Changes

Mann and Breen (1972) suggested that declining lobster abundance along eastern Nova Scotia released the sea urchin (*Strongylocentrotus droebachiensis*) from control by predation and allowed sea urchin populations to increase. This led to destructive grazing of kelp (*Laminaria*) by sea urchins which accounted for the large areas of relatively barren rock reported for many parts of the coastline. In addition to the importance of kelp to the coastal ecosystem in terms of primary productivity, kelp beds also contain populations of a variety of fish and invertebrates which virtually disappear when kelp disappears. Small lobsters may depend on kelp beds for shelter and food supply (Breen and Mann 1976a, 1976b). Sea urchins remain in the barren areas and graze algae as they settle, thus preventing reestablishment of the kelp beds and making the urchin-dominated barren grounds a stable feature of the ecosystem of the area (Breen and Mann 1976b; Chapman 1981).

A workshop concluded that data were insufficient to show that (1) destructive grazing by sea urchins is the sole cause of

kelp disappearance, (2) environmental factors were important in the decline of lobster abundance along eastern Nova Scotia, (3) lobsters are the prime predator of sea urchins, and (4) sea urchin populations increased due to release from predation by lobsters (Pringle et al. 1980).

Wharton and Mann (1981) challenged the workshop conclusions. They modified the original hypothesis that lobsters were a "keystone" predator in the system to one in which lobsters are considered to be one of a suite of predators that control sea urchin populations within kelp beds. It was shown that urchin-dominated barren grounds extended for more than 500 km along the eastern shore of Nova Scotia, and it was postulated that kelp cover had been much more extensive throughout the area in the past (Wharton and Mann 1981). They suggested that increased sea urchin abundance and resulting kelp bed destruction started in the north of the area (near Chedabucto Bay) in the late 1950's and progressed southward along the coast to kelp beds near Cape Sable in 1979. Lobster landing data showed that fishery collapse occurred in the same progression along the coast (i.e. kelp bed destruction and falling lobster catches were correlated).

Wharton and Mann (1981) concluded that kelp bed destruction led to a decrease in lobster productivity on account of (1) loss of cover, which increases the exposure of young lobsters to their predators, and (2) loss of productivity in the food web. They acknowledged Dadswell's (1979) and Robinson's (1979) explanations for the lobster recruitment failure but maintained that kelp bed destruction must have been a contributing factor.

Along most of eastern Nova Scotia, widespread mass mortalities of sea urchins, apparently caused by a species-specific, waterborne pathogen, occurred during the autumns of 1980 and 1981 (Miller and Colodey 1983). The kill was nearly complete along 160 km of shoreline (straight-line distance) and was intermittent along another 280 km. Further mass mortalities occurred in 1982 (Scheibling and Stephenson 1984) and 1983 (Miller 1985a). An extensive survey in 1982 revealed that algal recolonization was proceeding rapidly in formerly barren areas (Moore and Miller 1983; Miller 1985a). However, recovery of the sea urchin population has already begun (Miller 1985b).

Miller (1985c) considered that increased lobster landings for eastern Nova Scotia, beginning in 1979 and accelerating in 1983 (Fig. 3A), were unrelated to algal recolonization which was modest until 1982. If kelp recovery has had a positive effect on lobster productivity, it would not be evident in lobster landings until the mid- or late 1980's (Miller 1985c).

In his reappraisal of the lobster–urchin–seaweed interaction of eastern Nova Scotia, Miller (1985c) concluded that a positive relationship between kelp and lobster productivity has only weak support from available data. However, until proof to the contrary becomes available, it seems likely that ecosystem changes of the kind that have occurred along eastern Nova Scotia would cause some variability in recruitment to standing stocks of lobsters.

## Larval Recruitment Processes

Plankton sampling has demonstrated that the four free-swimming larval stages of the American lobster concentrate at or near (within 1 m) the water surface. Under bright sunshine and also at night there is limited dispersal from the surface water layer (Templeman 1937, 1939; Templeman and Tibbo 1945; Scarratt 1973; Harding et al. 1982; Stasko 1980b; Phillips and Sastry 1980). Because of this strong affinity for the surface layer, it was concluded that dispersal of lobster larvae from the parental stock location was controlled by surface water drift (Templeman 1937, 1939; Templeman and Tibbo 1945; Scarratt 1964). Most of the recent considerations of recruitment processes (i.e. mechanisms that determine where larvae eventually settle) for the lobster are based on the assumption that larvae are more or less passive current drifters and are transported downstream by surface currents, the distance depending on current velocity and the time required for development to the settling stage as determined primarily by temperature. Therefore, the larvae that settle and recruit to the population in a given area would originate somewhere upstream.

On the basis of residual surface current patterns, Dadswell (1979) delineated six large recruitment cells around the Maritimes. These are of two types: open or longitudinal cells (numbered 1–4 in Fig. 5) and closed or circular cells (numbered 5 and 6 in Fig. 5). He characterized longitudinal cells as generally having oscillating recruitment and high susceptibility to environmental perturbation but with some stability towards the downstream end of the cell. Closed cells, on the other hand, he suggested would be less susceptible to environmental perturbation and would have more stable recruitment. His analyses of lobster landing trends by area tended to support these generalizations.

Stasko (1978) hypothesized that larvae produced offshore on southern Scotian Shelf (Browns Bank) are carried by prevailing surface currents and contribute to recruitment in the inshore area of southwestern Nova Scotia. In turn, tagging studies show that larger inshore animals migrate offshore in this area (Stasko 1980c; Campbell and Stasko 1985). This possibility was one of Dadswell's (1979) arguments for a closed recruitment cell for southwestern Nova Scotia.

Harding et al. (1983) concluded that stage IV larvae found in the inshore area of southwestern Nova Scotia are spawned elsewhere. Their calculations were based on average sea surface temperatures and residual current speeds and directions available from the literature for the area as well as larval development rates in relation to temperature (from Templeman 1936b). These indicate that recruitment in the inshore area of southwestern Nova Scotia is derived from offshore stocks on the northern face of Georges Bank rather than Browns Bank as suggested by Stasko (1978). They further suggested that all regions bordering on the Gulf of Maine gyre are within one recruitment system.

Harding et al. (1983) suggested that Georges Bank together with the southern Gulf of Maine and the southern Gulf of St. Lawrence are warmwater nursery areas with plenty of food for larval lobsters which supply larvae to neighboring regions where temperatures are too low for locally produced larvae to provide significant recruitment. In addition to the inshore area of southwestern Nova Scotia already mentioned, the eastern shore of Nova Scotia probably has a marginal climate for successful larval recruitment. Residual current patterns indicate that the most likely source of larvae in this area is the Gulf of St. Lawrence via warmwater outflow around Cape Breton Island (Harding et al. 1983).

Residual surface drift from northwest to southeast is considered to be a strong influence on larval recruitment patterns in the Northumberland Strait area of the southern Gulf of St. Lawrence (Iles 1975; Dadswell 1979; Harding et al. 1983). In St. Georges Bay at the eastern end of Northumberland Strait,

the presence of a gyre is considered to act as a retention mechanism for larvae produced there (Harding et al. 1982).

In attempting to explain variability in larval abundance in a nearshore area in relation to wind direction, Squires (1965, 1970) and Squires et al. (1971) suggested the possibility that lobster larvae may be capable of maintaining position near parental grounds and that detection of turbulence induced by wind or by surf close to shore may trigger vertical movements. These would enable larvae to utilize currents moving in different directions at different depths as a mechanism whereby long-distance displacement by surface currents is avoided. Caddy (1979) defined centers of distribution for each of the four larval stages in each year and found that, in general, for stage IV larvae it was 20–40 km to the westward of that for earlier stages despite a prevailing southwesterly wind. To account for this, he suggested that later larval stages make use of some behavioral and hydrographic mechanisms to maintain position or even to move to windward. Specifically, he suggested that at least the later larval stages move vertically presumably at night to a depth where a countercurrent results in upstream transport in relation to the surface. He concluded that there was little evidence for drift of larvae into or out of the survey area and that larvae present result predominantly from local spawning.

In surveys conducted in the Georges Bank – Gulf of Maine area in 1983 and 1984, all four larval stages were caught throughout the upper 30 m of the water column (G. C. Harding, Marine Ecology Laboratory, Dartmouth, N.S., pers. comm.). For stages I and II there was evidence of day/night shifts in vertical distribution. The observations suggest that lobster larvae move vertically within the near-surface layer to a much greater extent than previous studies indicate.

There is an extensive literature which demonstrates that, for a wide variety of decapod crustacea, behavioral responses of larvae to environmental stimuli, such as gravity, light, temperature, salinity, and hydrostatic pressure as well as activity rhythms, play a key role in depth distribution and vertical movements. Sulkin (1984) provided a comprehensive review for brachyuran crabs and Phillips (1981) for the Western Australian rock lobster. Various recruitment processes in which larval behavior is an essential component have been proposed for a number of decapod crustacea. Ennis (1983b) provided a review. American lobster larvae have well-developed behavioral responses (Phillips and Sastry 1980 for review) which have been shown to be involved in recruitment in other decapod crustacea, and it is unlikely that passive drift by surface currents would be the basis of larval recruitment processes in this species. As for other species, larval recruitment processes in the American lobster probably involve a complex interaction of behavioral, ecological, and physical oceanographic factors.

## Summary

Evidence from tagging, morphometric and electrophoretic studies, analyses of fishery landing trends, and differences in population parameters demonstrates that the American lobster is divided into a number of different stocks. These stocks occur over broad geographical areas between which precise boundaries cannot be defined at present and which are too large to be practical as fishery management units.

Lobster fisheries are regulated separately in many small areas. Since ineffective management in one area of a stock could have repercussions elsewhere, it is important that the consequences of different management regimes be known and considered in order that overall conservation requirements of a stock can be met.

Annual landings fluctuate in all major lobster fishing areas as a result of variability in recruitment to standing stocks. Recruitment variation appears to be caused mainly by temperature variation, variation in annual river discharge, and fishery-induced variability in egg production. Ecosystem changes may also be important, and in one area, man-made interruption in larval supply may have been a factor contributing to variation in recruitment.

Currently there are two hypotheses regarding larval recruitment processes in the American lobster. One is based on the assumption that larvae are passive current drifters and, since they concentrate near the surface, are transported by surface currents. This hypothesis considers that larvae which settle in an area originate somewhere upstream, the distance depending on current velocity and the time required for development to the settling stage. The second hypothesis suggests that larvae undergo vertical movements which enable them to utilize currents moving in different directions to maintain position near parental grounds. Lobster larvae have well-developed behavioral responses which have been shown to be involved in recruitment in other decapod crustacea. As for other species, larval recruitment processes in the American lobster probably involve a complex interaction of behavioral, ecological, and physical oceanographic factors.

The prospect of recruitment failure because of low levels of egg production under current management regimes makes an understanding of stock and recruitment for consideration in the fisheries management process vitally important. The potential for substantial increases in egg production is obvious. However, there is no basis for predicting the extent to which increased egg production will affect subsequent recruitment to standing stocks. Considering the imprecision associated with stock definition, the extent to which factors other than spawning stock size seem to cause variability in recruitment, and the lack of understanding of larval recruitment processes, determination of a stock–recruitment relationship for the American lobster is unlikely in the near future.

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## References

ANONYMOUS 1975. Lobster Fishery Task Force Final Report, March 1975, Halifax, N.S.

1977. Report of the Working Group on *Homarus* stocks. International Council for the Exploration of the Sea, Council Meeting 1977/K:11, Copenhagen, Denmark.

1978. Draft American lobster fishery management plan, June 26, 1978. Prepared by Lobster Sub-Board of the Northeast Marine Fisheries Board.

1979. Report of the *Homarus* Working Group, International Council for the Exploration of the Sea, Council Meeting 1979/K:8, Copenhagen, Denmark.

ANTHONY, V. C. 1980. Review of lobster mortality estimates in the United States. Can. Tech. Rep. Fish. Aquat. Sci. 932: 17–25.

BARLOW, J., AND J. RIDGWAY. 1971. Polymorphisms of esterase isozymes in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 28: 15–21.

BOOKE, H. E. 1981. The conundrum of the stock concept — are nature and nurture definable in fisheries science? Can. J. Fish. Aquat. Sci. 38: 1479–1480.

BOUDREAULT, F.-R., J.-N. DUPONT, AND C. SYLVAIN. 1977. Modèles linéaires de prédiction des débarquements de homard aux Iles-de-la Madeleine (Golfe du Saint-Laurent). J. Fish. Res. Board Can. 34: 379–383.

BREEN, P. A., AND K. H. MANN. 1976a. Destructive grazing of kelp by sea urchins in eastern Canada. J. Fish. Res. Board Can. 33: 1278–1283.

1976b. Changing lobster abundance and the destruction of kelp beds by sea urchins. Mar. Biol. 34: 137–142.

BUGDEN, G. L., B. T. HARGRAVE, M. M. SINCLAIR, C. L. TANG, J.-C. TERRIASULT, AND P. A. YEATS. 1982. Freshwater runoff effects in the marine environment: the Gulf of St. Lawrence example. Can. Tech. Rep. Fish. Aquat. Sci. 1078: 89 p.

CADDY, J. F. 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 204–216.

CAMPBELL, A. 1980. A review of mortality estimates of lobster populations in the Canadian Maritimes. Can. Tech. Rep. Fish. Aquat. Sci. 932: 28–35.

1983. Growth of tagged American lobsters, *Homarus americanus*, in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 40: 1667–1675.

1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. Can. J. Fish. Aquat. Sci. 43: 2197–2205.

CAMPBELL, A., AND R. K. MOHN. 1983. Definition of American lobster stocks for the Canadian Maritimes by analysis of fishery landing trends. Trans. Am. Fish. Soc. 112: 744–759.

CAMPBELL, A., AND D. G. ROBINSON. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes. Can. J. Fish. Aquat. Sci. 40: 1958–1967.

CAMPBELL, A., AND A. B. STASKO. 1985. Movements of tagged American lobsters, *Homarus americanus*, off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 42: 229–238.

1986. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. Mar. Biol. (In press)

CHAPMAN, A. R. O. 1981. Stability of sea-urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada. Mar. Biol. 62: 307–311.

COOPER, R. A., AND J. R. UZMANN. 1980. Ecology of juvenile and adult *Homarus* p. 97–142. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

DADSWELL, M. J. 1979. A review of the decline in lobster (*Homarus americanus*) landings in Chedabucto Bay between 1956 and 1977 with an hypothesis for a possible effect by the Canso Causeway on the recruitment mechanism of eastern Nova Scotia lobster stocks. Fish. Mar. Serv. Tech. Rep. 834 (Part 3): 114–144.

DOW, R. L. 1969. Cyclic and geographic trends in seawater temperature and abundance of American lobster. Science (Wash., DC) 164: 1060–1063.

1974. American lobsters tagged by Maine commercial fishermen, 1957–59. Fish. Bull. U.S. 72: 622–623.

1977. Relationship of sea surface temperature to American and European lobster landings. J. Cons., Cons. Int. Explor. Mer 37: 186–190.

1978. Effects of sea surface temperature cycles on landings of American, European, and Norway lobsters. J. Cons., Cons. Int. Explor. Mer 38: 271–272.

1980. The clawed lobster fisheries, p. 265–316. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

ENNIS, G. P. 1980. Recent and current Canadian research on growth of lobsters in the wild, p. 45–48. *In* V. C. Anthony and J. F. Caddy [ed.] Proceedings of the Canada–US Workshop on Status of Assessment Science for N.W. Atlantic Lobster (*Homarus americanus*) Stocks (St. Andrews, N.B., Oct. 24–26, 1978). Can. Tech. Rep. Fish. Aquat. Sci. 932: vii + 186 p.

1982. The Newfoundland lobster fishery: a review of statistics, stock status and current management considerations. Can. MS Rep. Fish. Aquat. Sci. 1666: iv + 11 p.

1983a. Annual variations in standing stock in a Newfoundland population of lobsters. N. Am. J. Fish. Manage. 3: 26–33.

1983b. The effect of wind direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland near-shore area. Can. Tech. Rep. Fish. Aquat. Sci. 1138: iv + 19 p.

ENNIS, G. P., P. W. COLLINS, AND G. DAWE. 1982. Fisheries and population biology of lobsters (*Homarus americanus*) at Comfort Cove, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1116: iv + 45 p.

FLOWERS, J. M., AND S. B. SAILA. 1972. An analysis of temperature effects on the inshore lobster fishery. J. Fish. Res. Board Can. 29: 1221–1225.

FOGARTY, M. J. 1984. Temperature–yield relationships for the Maine American lobster (*Homarus americanus*) fishery: a time series analysis approach. NAFO SCR Doc. 84/VI/57: 23 p.

FOGARTY, M. J., D. V. D. BORDEN, AND H. J. RUSSELL. 1980. Movements of tagged American lobster, *Homarus americanus*, off Rhode Island. Fish. Bull. U.S. 78: 771–780.

HARDING, G. C., K. F. DRINKWATER, AND W. P. VASS. 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and the Gulf of Maine: a new synthesis. Can. J. Fish. Aquat. Sci. 40: 168–184.

HARDING, G. C., W. P. VASS, AND K. F. DRINKWATER. 1982. Aspects of larval lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia. Can. J. Fish. Aquat. Sci. 39: 1117–1129.

IHSSEN, P. E., H. E. BOOKE, J. M. CASSELMAN, J. MCGLADE, N. R. PAYNE, AND F. M. UTTER. 1981. Stock identification: materials and methods. Can. J. Fish. Aquat. Sci. 38: 1838–1855.

ILES, T. D. 1975. An analysis of the decline in the southern Gulf of St. Lawrence lobster landings to demonstrate differential area and time effects. ICES Shellfish Committee C.M.1975/K:55, Copenhagen, Denmark.

MACLEAN, J. A., AND D. O. EVANS. 1981. The stock concept, discreteness of fish stocks and fisheries management. Can. J. Fish. Aquat. Sci. 38: 1889–1898.

MANN, K. H., AND P. A. BREEN. 1972. The relation between lobster abundance, sea urchins, and kelp beds. J. Fish. Res. Board Can. 29: 603–609.

MCCRACKEN, F. D. [ED.]. 1979. Editor's note, p. 145. *In* Canso marine environment workshop; Part 3 of 4 parts, Fishery impacts. Fish Mar. Serv. Tech. Rep. 834.

MILLER, R. J. 1985a. Sea urchin pathogen: a possible tool for biological control. Mar. Ecol. Prog. Ser. 21: 169–174.

1985b. Succession in sea urchin and seaweed abundance in Nova Scotia, Canada. Mar. Biol. 84: 275–286.

1985c. Seaweeds, sea urchins, and lobsters: a reappraisal. Can. J. Fish. Aquat. Sci. 42: 2061–2072.

MILLER, R. J., AND A. G. COLODEY. 1983. Widespread mass mortalities of the green sea urchin in Nova Scotia, Canada. Mar. Biol. 73: 263–267.

MOORE, D. S., AND R. J. MILLER. 1983. Recovery of macroalgae following widespread sea urchin mortality with a description of the shallow, hard-bottom habitat on the Atlantic coast of Nova Scotia. Can. Tech. Rep. Fish. Aquat. Sci. 1230: 94 p.

MORRISSEY, T. D. 1971. Movements of tagged American lobsters, *Homarus americanus*, liberated off Cape Cod, Massachusetts. Trans. Am. Fish. Soc. 100: 117–120.

ODENSE, P. H., AND C. ANNAND. 1978. Isoenzyme systems of an inshore and offshore lobster population. ICES Shellfish Committee C.M.1978/K:15, Copenhagen, Denmark.

ORACH-MEZA, F. L., AND S. B. SAILA. 1978. Application of a polynomial distributed lag model to the Maine lobster fishery. Trans. Am. Fish. Soc. 107: 402–411.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

PHILLIPS, B. F., AND A. N. SASTRY. 1980. Larval ecology, p. 11–57. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 2. Academic Press, New York, NY. 390 p.

PRINGLE, J. D., AND R. E. DUGGAN. 1984. Latent lobster fishing effort along Nova Scotia's Atlantic coast. CAFSAC Res. Doc. 84/56: 23 p.

PRINGLE, J. D., G. J. SHARP, AND J. F. CADDY [ED.]. 1980. Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant/animal harvesting. Can. Tech. Rep. Fish. Aquat. Sci. 954: 273 p.

ROBINSON, D. G. 1979. Consideration of the lobster (*Homarus americanus*) recruitment overfishing hypothesis; with special reference to the Canso Causeway. Fish. Mar. Serv. Tech. Rep. 834: 77–99.

ROGERS, B. A., J. S. COBB, AND N. MARSHALL. 1968. Size composition of inshore and offshore larvae of the lobster, *Homarus americanus*, off southern New England. Proc. Natl. Shellfish. Assoc. 58: 78–81.

RUSSELL, H. J. 1980. The determination of growth rates for American lobsters. Can. Tech. Rep. Fish. Aquat. Sci. 932: 1–7.

SAILA, S. B., AND J. M. FLOWERS. 1969. Geographic morphometric variation in the American lobster. Syst. Zool. 18: 330–338.

SCARRATT, D. J. 1964. Abundance and distribution of lobster larvae (*Homarus*

*americanus*) in Northumberland Strait. J. Fish. Res. Board Can. 21: 661–680.

1973. Abundance, survival, and vertical and diurnal distribution of lobster larvae in Northumberland Strait, 1962–1963, and their relationships with commercial stocks. J. Fish. Res. Board Can. 30: 1819–1824.

SCHEIBLING, R. E., AND R. S. STEPHENSON. 1984. Disease related mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. Mar. Biol. 78: 153–164.

SHELDON, R. W., W. H. SUTCLIFFE JR., AND K. DRINKWATER. 1982. Fish production in multispecies fisheries, p. 28–34 *In* M. C. Mercer [ed.] Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59: 169 p.

SQUIRES, H. J. 1965. Decapod crustaceans of Newfoundland, Labrador and the Canadian eastern Arctic. Fish. Res. Board Can. MS Rep. 810: 201 p.

1970. Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland 1960–65. Proc. Natl. Shellfish. Assoc. 60: 22–39.

SQUIRES, H. J., G. E. TUCKER, AND G. P. ENNIS. 1971. Lobster (*Homarus americanus*) in Bay of Islands, Newfoundland, 1963–65. Fish. Res. Board Can. MS Rep. 1151: 58 p.

STASKO, A. B. 1978. Inshore–offshore SW Nova Scotia lobster stock interaction: an hypothesis. CAFSAC Res. Doc. 78/37: 10 p.

1980a. Possible causes for decline of lobster landings in Northumberland Strait. CAFSAC Res. Doc. 80/3: 7 p.

1980b. Lobster larval surveys in Canada. Can. Tech. Rep. Fish. Aquat. Sci. 932: 157–169.

1980c. Tagging and lobster movements in Canada. Can. Tech. Rep. Fish. Aquat. Sci. 932: 141–150.

SULKIN, S. D. 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. Mar. Ecol. Prog. Ser. 15: 181–205.

SUTCLIFFE, W. H. JR. 1972. Some relations of land drainage, nutrients, particulate material and fish catch in two eastern Canadian Bays. J. Fish. Res. Board Can. 29: 357–362.

1973. Correlations between seasonal river discharge and local landings of American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 30: 856–859.

TEMPLEMAN, W. 1935. Local differences in the body proportions of the lobster, *Homarus americanus*. J. Biol. Board Can. 1: 213–226.

1936a. Local differences in the life history of the lobster (*Homarus americanus*) on the coast of the Maritime provinces of Canada. J. Biol. Board Can. 2: 41–88.

1936b. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J. Biol. Board Can. 2: 485–497.

1937. Habits and distribution of larval lobsters (*Homarus americanus*). J. Biol. Board Can. 3: 343–347.

1939. Investigations into the life-history of the lobster (*Homarus americanus*) on the west coast of Newfoundland, 1938. Nfld. Dep. Nat. Resour. Res. Bull. (Fish.) 7: 52 p.

1944. Abdominal width and sexual maturity of female lobsters on Canadian Atlantic coast. J. Fish. Res. Board Can. 6: 281–290.

TEMPLEMAN, W., AND S. N. TIBBO. 1945. Lobster investigations in Newfoundland 1938 to 1941. Nfld. Dep. Nat. Resour. Res. Bull. (Fish.) 16: 98 p.

TRACEY, L., K. NELSON, D. HEDGECOCK, R. A. SHLESER, AND M. L. PRESSICK. 1975. Biochemical genetics of lobsters: genetic variation and the structure of American lobster (*Homarus americanus*) populations. J. Fish. Res. Board Can. 32: 2091–2101.

UZMANN, J. R., R. A. COOPER, AND K. J. PECCI. 1977. Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the southern New England Continental Shelf. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-705: 92 p.

WHARTON, W. G., AND K. H. MANN. 1981. Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster, *Homarus americanus*, on the Atlantic coast of Nova Scotia. Can. J. Fish. Aquat. Sci. 38: 1339–1349.

WILDER, D. G. 1953. The growth rate of the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 10: 371–412.

1963. Movements, growth, and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. J. Fish. Res. Board Can. 20: 305–318.

# Implications of Fluctuations in Recruitment in Selected Crab Populations

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Jamieson, G. S. 1986. Implications of fluctuations in recruitment in selected crab populations. Can. J. Fish. Aquat. Sci. 43: 2085–2098.

Two general categories of crab fisheries exist, shallow-water, nearshore fisheries (e.g. *Cancer, Callinectes*) and deepwater, offshore fisheries (e.g. *Paralithodes, Chionoecetes*). Species in the former category are managed typically in a passive manner with no annual restriction of catch on the basis of population abundance, whereas species in the latter category tend to be managed actively through annual catch quotas. Active management of fisheries requires regular resource surveys and provides the most comprehensive data base for recruitment study. Recruitment fluctuations in crab populations are analyzed by considering (1) production of progeny from perceived parent populations, (2) mechanisms which determine magnitude of progeny return to fishery grounds, and (3) factors that determine survival of juveniles. It is concluded that year-class strength at recruitment can be established at any preceding life stage and that while one life stage may appear more critical than others for a given population in a given year, this is unlikely to be the case in future years or apply to different populations. There is little evidence that recruitment magnitude in crab populations has been influenced by past resource management. Management has not stabilized landings in any fishery over the long term, and environmental variables seem to be the major factor influencing recruitment level. The need for prediction of future fishery performance is greatest in actively managed fisheries, with short-term economic benefits and socially acceptable exploitation, not control of recruitment, being the most likely achievement of management.

Il existe deux grandes catégories de pêches du crabe, l'une qui se pratique en eau peu profonde près des côtes (p. ex. *Cancer, Callinectes*), et l'autre qui se pratique au large en eau profonde (p. ex. *Paralithodes, Chionoecetes*). Les espèces de la première catégorie font généralement l'objet d'une gestion passive sans restriction annuelle des prises en fonction de l'abondance de la population, alors que les espèces de la deuxième font l'objet d'une gestion active par l'imposition de quotas annuels de prises. La gestion active des pêches demande des relevés réguliers des ressources et offre la base de données la plus exhaustive pour les études sur le recrutement. Nous analysons les fluctuations du recrutement des populations de crabe en étudiant 1) la production de jeunes par une population considérée comme parente, 2) les mécanismes qui déterminent l'ampleur du retour de la progéniture sur les lieux de pêche et 3) les facteurs qui déterminent la survie des juvéniles. Nous en concluons que l'effectif de la classe annuelle au recrutement peut être calculé à n'importe lequel des stades antérieurs et que, si un stade peut sembler plus critique que les autres pour une population donnée au cours d'une année donnée, il est peu probable que ce soit le cas les années suivantes ou que cela s'applique à des populations différentes. Il est peu vraisemblable que l'ampleur du recrutement dans une population de crabe soit influencée par les mesures antérieures de gestion. À long terme, la gestion n'a stabilisé les débarquements dans aucune pêcherie, et les variables environnementales semblent constituer le principal facteur qui agit sur le recrutement. C'est dans les pêches qui font l'objet d'une gestion active qu'il est le plus nécessaire de prédire le rendement futur de la pêche, et la réussite de la gestion peut se manifester de façon bien supérieure dans les profits économiques à court terme et dans un mode d'exploitation socialement acceptable que dans une intervention sur le recrutement.

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Investigation of causes of significant fluctuations in abundance in commercially exploited stocks has received high priority because of associated economic consequences. Variation in abundance may be caused by the act of fishing and by the vast array of environmental and biotic factors intrinsic to the marine ecosystem. Initial studies of a population's reproductive success, or "year-class strength," generally focused on environmental factors because of the relative availability of such data. As biological data has accumulated, research has become more theoretical and oriented towards measuring overall production in relation to population size and rate of exploitation. From a management perspective, the usefulness of understanding population dynamics is determined by the accuracy and reliability of both predictions of recruitment and of the consequences of fishery-induced perturbations.

This paper reviews (1) the pattern and possible causative factors of fluctuations in recruitment in selected Northern Hemisphere crab stocks, (2) how managers have dealt with variable landings, and (3) the need for improved predictions of fluctuations in stock abundance.

## Life History

Intrinsic to our understanding of a parent/recruit relationship is knowledge about species' life history, spatial distribution of populations, and dispersal of progeny. These aspects assume

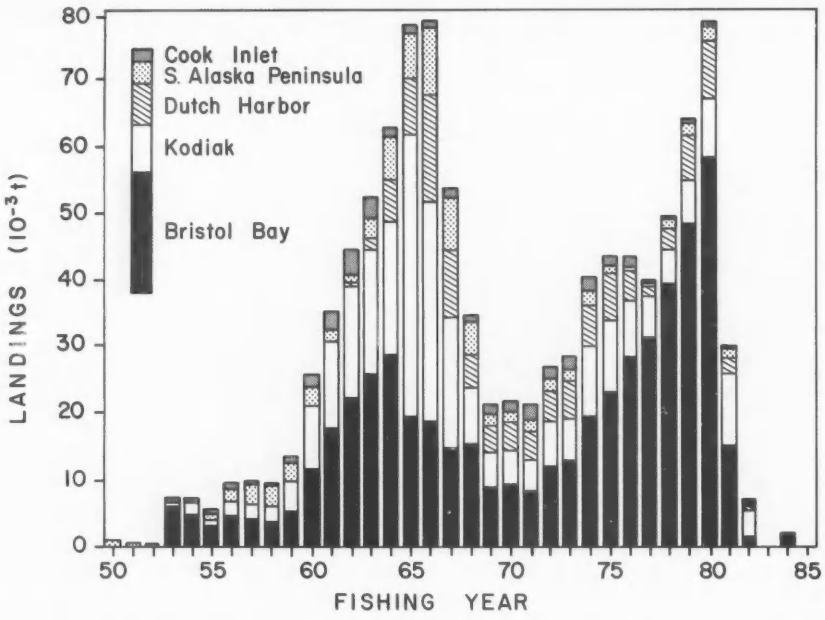


FIG. 1. Historical Alaskan red king crab landings from 1950 to 1984 in the Bristol Bay, Dutch Harbor, Alaska Peninsula, Kodiak, and Cook Inlet management areas (modified from Blau 1986).

particular importance with benthic invertebrates such as crawling decapods because of the relatively limited mobility (typically <100 km) of adults in contrast with that of the larval stages, which are usually pelagic.

In this paper, reference will be made to species supporting selected major North American and European crab fisheries: red king crab (*Paralithodes camtschatica*), tanner, or snow, crabs (*Chionoecetes bairdi* and *C. opilio*), Dungeness crab (*Cancer magister*), edible crab (*C. pagurus*), and blue crab (*Callinectes sapidus*). Life histories and exploitation features are briefly described to acquaint noncarcinologists with crab biology and past recruitment patterns.

## Red King Crab

Red king crab are distributed widely in continental shelf waters in the North Pacific from the Sea of Japan to British Columbia (Hart 1982; Jamieson and Sloan 1985). The major North American fishery for this species has been in the southeastern Bering Sea, where two red king crab stocks are recognized. Female and sublegal size male crabs are found closer to shore and somewhat east of most legal-size male crabs, i.e. where the fishery is centered (Otto 1981). Recruit abundance has fluctuated substantially in the last decade (Fig. 1), with most populations presently at minmum levels (Otto 1981; Blau 1986).

Larvae are pelagic for 98–112 d (Weber 1967), and transport of larvae by currents is thought to move them considerable distances from their hatching location. Abundance of juveniles in a given area may depend on larvae hatched elsewhere. For example, juveniles in the southeastern Bering Sea may partly originate from areas south of the Alaska Peninsula (Hebard 1959; Haynes 1974). There is relatively little information on life history and distribution of early juveniles (Armstrong et al. 1983). Sexual maturity is reached at about 5–6 yr of age; males are mature for 2–3 yr before recruitment to the fishery at about 8 yr of age. Females are not fished and, since they have no seminal vesticles, must molt and be mated again to produce new progeny.

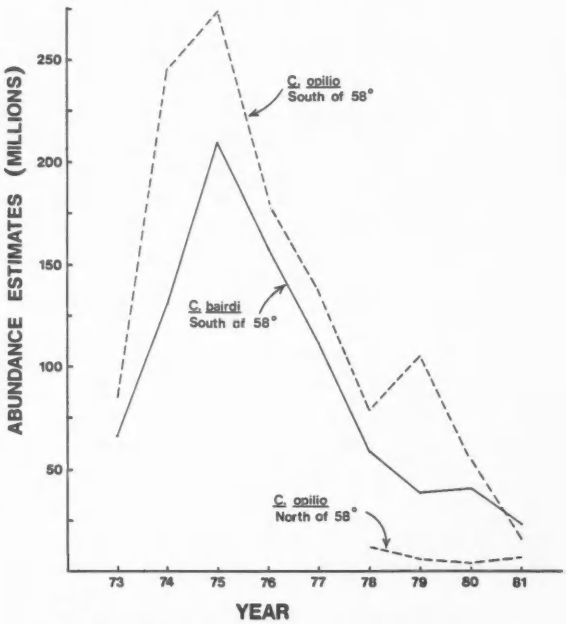


FIG. 2. Abundance estimates of tanner crabs derived from recent National Marine Fisheries Service trawl surveys (from Otto 1982).

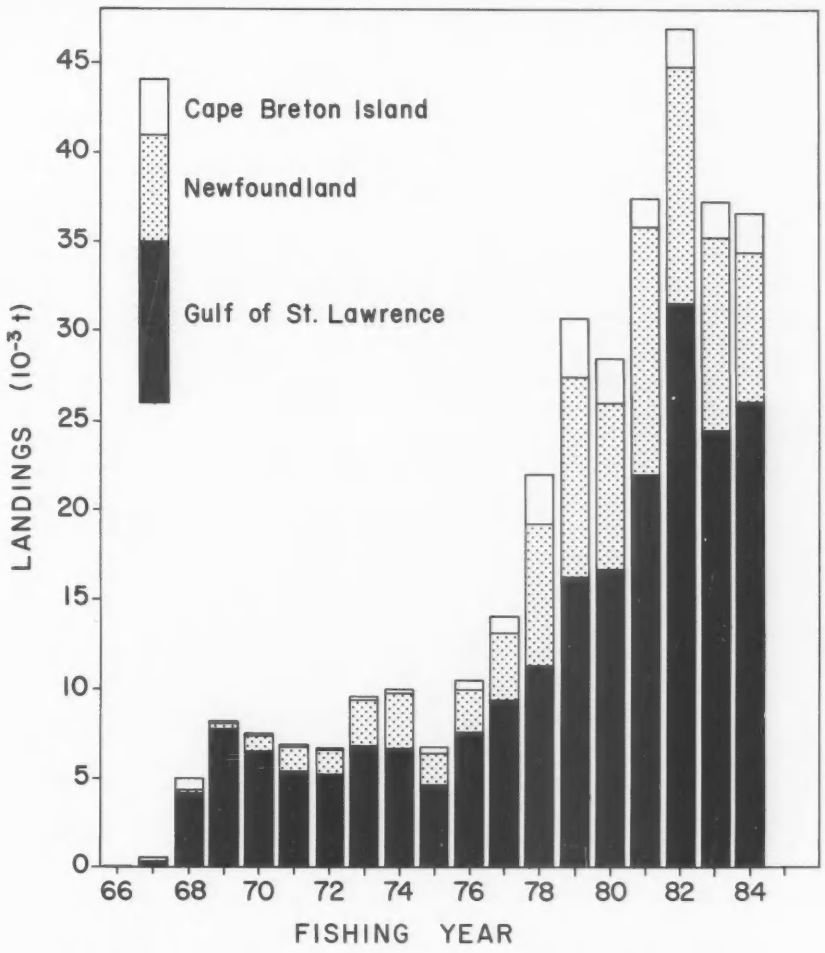


FIG. 3. Snow crab landings from Atlantic Canada, 1966–84 (R. Elner, pers. comm.).

Tanner (Snow) Crab

In the Pacific, *Chionoecetes* species are generally referred to as tanner crab, whereas in the western Atlantic, the only species exploited, *C. opilio*, is referred to as snow crab. This distinction will be used in this paper to differentiate between these two stocks.

In the eastern Pacific, *C. bairdi* ranges from the southeastern Bering Sea to Oregon whereas *C. opilio* is found only in the Bering Sea (Hart 1982). In the eastern Bering Sea, *C. bairdi* and *C. opilio* are both widely distributed and exploited. *Chionoecetes bairdi* populations were at relatively high abundance levels in the periods 1959–63, 1968–69, and 1974–76 (Otto 1981), but abundance has declined greatly after 1975 and has remained relatively low to the present (Fig. 2). There is little information on population size of *C. opilio* in the Pacific prior to the inception of a domestic fishery in about 1978, and since then it has followed the same basic pattern as described above for *C. bairdi* (Otto 1981). Single stocks of *C. bairdi* and *C. opilio* have been assumed for management purposes.

Larvae of *Chionoecetes* are pelagic for about 90 d and little is known about larval dispersal and juvenile ecology and distribution (Adams 1979). Reproduction is similar to that of king crabs, but females have a terminal puberty molt at sexual maturity. However, females can successfully mate in a hard shell condition, even while carrying a full clutch of eggs (Taylor et al. 1984). Females are not exploited in either species. Male *C. bairdi* and *C. opilio* become sexually mature in the eastern Bering Sea at least 1 yr before they can be legally exploited (Somerton 1981).

In Atlantic Canada, commercial fisheries for *C. opilio* are located in the Gulf of St. Lawrence, around Cape Breton, and off the east coast of Newfoundland. Exchange of adults between major fishing areas appears unlikely, but because of the extensive larval pelagic phase, larval settlement in an area from remote parental stocks may be possible (Elner 1982). Electrophoretic, morphormetic, and meristic analyses (Elner 1982) support the hypothesis of two separate snow crab stocks in Atlantic Canada, one in the Gulf of St. Lawrence and the other off Newfoundland. In all major fishing areas except Newfoundland, landings have increased since the inception of the fishery, and the major fluctuations in abundance observed in the Bering Sea have not been evident (Fig. 3). Landings in

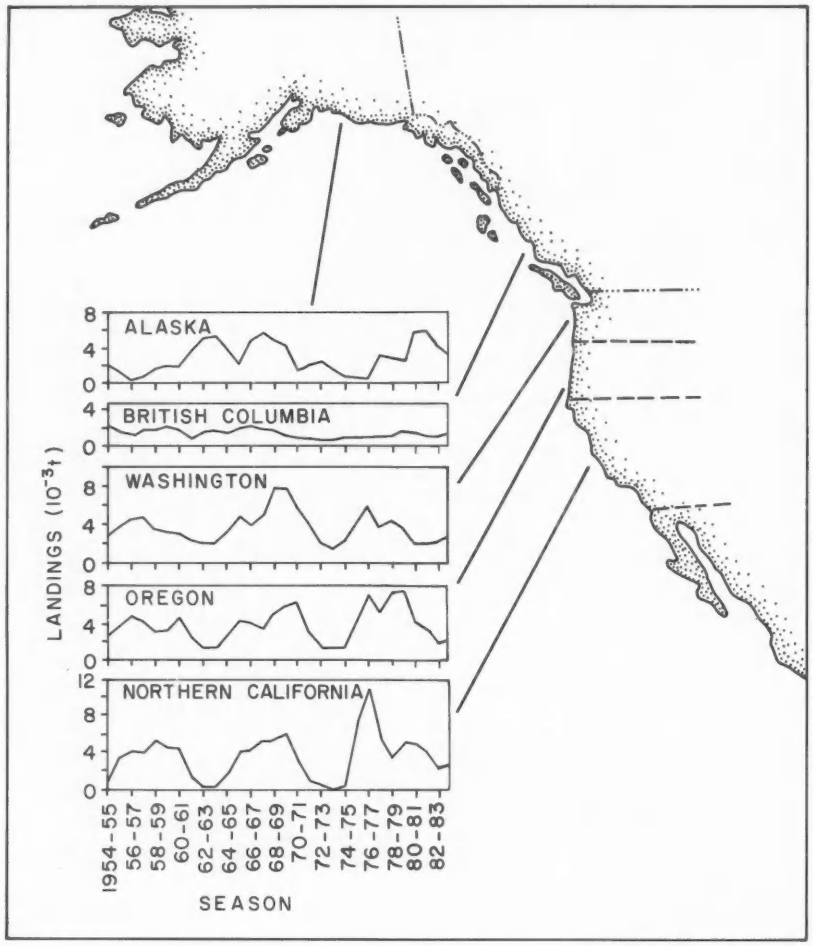


FIG. 4. Commercial landings of Dungeness crab by fishing season from Alaska to northern California, with the exception that Alaska and British Columbia landings are for calendar years, i.e. 1954–55 = 1955 (updated from Wild 1983).

Newfoundland have decreased since 1983 but still remain substantial. Females are not exploited.

## Dungeness Crab

Dungeness crab range from the Aleutian Islands to northern Mexico (Hart 1982) in the eastern Pacific, and commercially exploited populations occur from central California to Kodiak Island, Alaska. Except for Alaska (Eaton 1985), most crab populations are fully exploited, with annual catch generally reflecting crab abundance but not necessarily year-class strength, as contributions may be made from two or more cohorts (Methot and Botsford 1982; Botsford 1984; Hankin 1985). Historical landings (Fig. 4) have fluctuated cyclically in southern areas (see Hankin 1985 and Botsford 1986 for reviews) but this pattern has not been as evident in the catch data of more northern fisheries, where catch may not represent recruitment as closely (Jamieson 1985; Koeneman 1985; Eaton 1985). In southern fisheries, landings are currently at a low level.

Larvae are pelagic for about 105–125 d (Reilly 1983, 1985), and along the California to Washington coast, zoea may move offshore during the northward flowing Davidson Current period. It has been suggested that larvae hatching in southern areas could be transported a considerable distance by the time they settled out (Reilly 1983, 1985). Shallow-water areas are locations of high juvenile and adult abundance. Male crabs enter the fishery at 4 and 5 yr of age (Botsford 1984), 1–2 yr after they become sexually mature. Female crabs above the minimum legal size can be exploited only in British Columbia.

## Edible Crab

*Cancer pagurus* is the main species of crab fished regularly in European waters. Major fisheries for this species occur from Norway to Brittany (Fig. 5), with smaller fisheries occurring off Spain, Portugal, and Ireland (Edwards 1979). Traditional English fishing grounds have been inshore, but exploitation now occurs up to 60 km offshore (Brown and Bennett 1980). In the English Channel, landings and catch rates vary season-

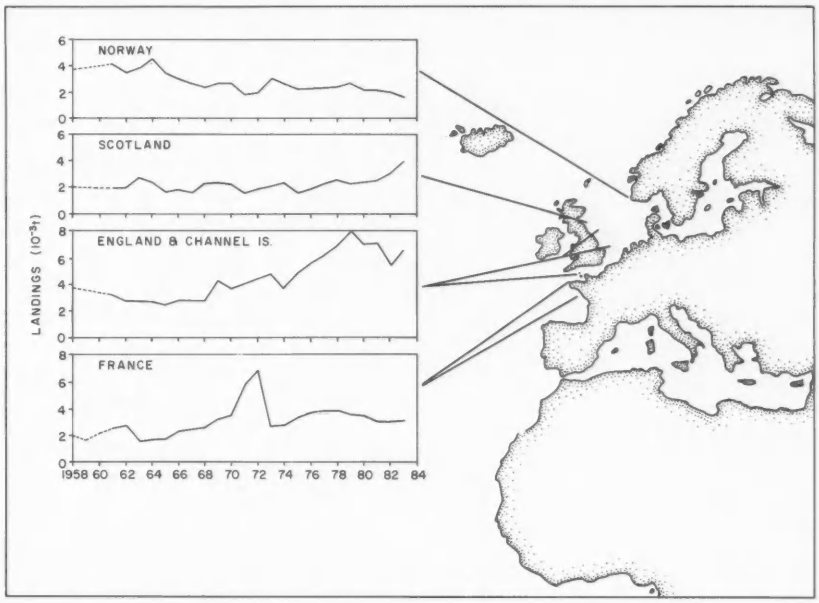


FIG. 5. Annual commercial landings of edible crab by country from 1958 to 1983 (from FAO Yearbrook of Fishery Statistics, Vol. 22–56).

ally, with the main fishery being offshore off Devon in the fall directed towards large, mature female crabs with developing gonads. The trend in landings has been effort-related since effort increased in the 1970's (C. Bannister, pers. comm.). Large, mature males up to 267 mm carapace width (CW) are caught, particularly inshore, in the spring (Brown and Bennett 1980).

Larvae are pelagic for about 23–30 d (Edwards 1979). Male and female crabs reach sexual maturity at 110 and 127 mm CW, respectively (Edwards 1979). Size selection by fishermen is dependent on market preferences, with the mean 50% selection point for males and females being 153 and 146 mm CW, respectively. The legal minimum size in England is 115 mm CW, much smaller than the size the market usually demands, and so selection is not knife-edged, in contrast with the other crab fisheries discussed here.

## Blue Crab

*Callinectes sapidus* occurs from Massachusetts to Uruguay (Norse 1977) and is fished in both deep channels in estuaries and the brackish waters of their river tributaries. In the United States, Chesapeake Bay has been a major fishing location, providing about 40% of American landings, and while landings have fluctuated in size, they have always remained substantial (Fig. 6).

Mated females leave low-salinity waters and migrate to the mouths of bays in spring and fall (Perry 1975; Van Engel 1958), where in Chesapeake Bay, they extrude eggs 2–9 mo later. Adult males remain in brackish waters throughout their lives. Larvae are pelagic for 36–60 d and are abundant in coastal marine waters (Smyth 1980; McConaugha et al. 1983) and, in some years, in large bays such as Chesapeake Bay (W. Van Engel, pers. comm). Recently, there have been numerous studies investigating mechanisms of return of larval or postlarval stages to estuaries where the adult population is found (Epifanio et al. 1984; Johnson 1982; Johnson et al. 1984; Hester 1983; Sulkin and Van Heukelem 1982; Sulkin et al. 1980).

Crabs mature at 1–1.5 yr of age and only live 1 more yr. Landed crab range in size from 112 to 204 mm CW (Perry 1975), with a minimum legal size for males in the United States of 127 mm CW. The size limit for females is the same as that for males, except in Virginia and Maryland where there is no minimum size limit for adult females.

It is evident from these brief descriptions of species biology, fisheries, and management that while crabs are a diverse group, they have two predominant characteristics not shared with lobsters. Firstly, some commercially exploited crabs, notably king and tanner (snow) crabs, only occur in abundance in deep water and/or offshore locations, in contrast with the shallow-water, nearshore habitat preferences of most lobster populations. Fisheries for these crab species have only developed in the last few decades because of the required sophistication of fishing vessels and techniques, making the time series of landings data available for study of recruitment variability relatively short. Study of the biology of deepwater species, particularly spatial distributions and juvenile survival, is difficult logistically and has only just begun to be attempted. Secondly, with all commercially exploited crab species, mature females are usually much smaller than mature males and hence are not exploited. Fishing gear is designed typically to facilitate the escape of small crabs, and so biological data about female distribution, biology, and the reproductive capacity of the population are relatively limited for most crab species. Because commercial catch data provide little information on female crabs, their study typically requires directed research with specialized gear. Generally limited resources for intensive study of nearshore crab populations (particularly unexploited cohorts) and the difficulty in analyzing data obtained from different fishing

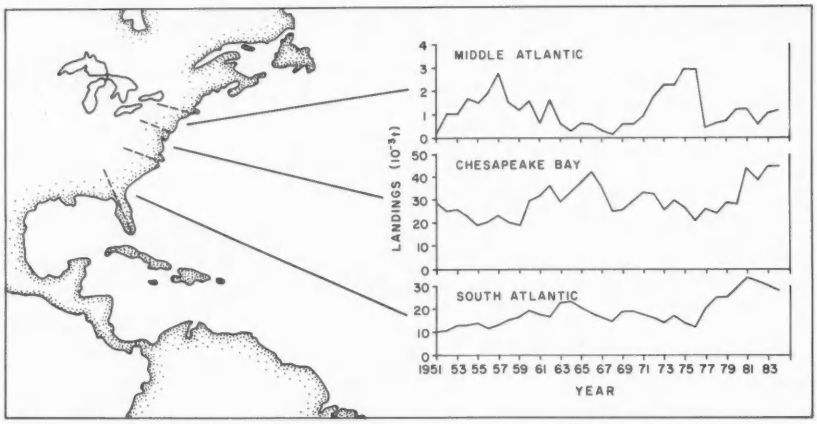


FIG. 6. Annual commercial landings of hard-shell blue crab from the eastern United States (Middle Atlantic = New York, New Jersey, Delaware; Chesapeake Bay = Maryland, Virginia; South Atlantic = North Carolina, South Carolina, Georgia, Florida) (from NMFS Statistical Digest, 1951–76; state and federal fisheries personnel, pers. comm., 1977–84).

methods has resulted to date in few comprehensive studies of crab reproductive success.

## Recruitment: Its Characteristics

The reproductive success achieved by a population can be assessed at any stage in the development of progeny: eggs, zoeae, megalops, juveniles, and ultimately adults. For the purpose of this paper, reproduction is defined as the number surviving to a specified size or theoretical age. I use the term "theoretical" since, because crustaceans molt, there is no method to establish the ages of later life stages accurately; age is estimated from growth models (e.g. Von Bertalanffy) or population size frequency data. Recruitment in a given year is defined as the number of crabs, usually of a specified year-class, surviving and through growth, adding to numbers in the exploited size class that year. Recruitment is thus a measure of successful reproduction to the size at which crabs enter the fishery, and at this crab size, the terms reproduction and recruitment are synonymous. A reproduction (recruitment) curve is the number at a specified size or age from spawning plotted against the abundance of the parent population which produced them.

To develop an understanding of factors influencing recruitment, three points require investigation and are presented in the following sections.

### Production of Progeny from a Perceived Parent Population

Our theoretical understanding of the population dynamics of any species requires that a reasonable level of larval production is essential if optimal fishery yields are to be achieved. To achieve this, it is desirable to maintain female abundance in the perceived parent population within some hypothesized acceptable range.

### Mechanisms that Determine Magnitude of Progeny Return to Fishery Grounds

All crab species discussed here have a sufficiently long planktonic larval stage to achieve wide dispersal of progeny. Egg hatching locations and/or locations of larval abundance are often geographically removed from habitats favourable for survival of juveniles, which in turn may differ from areas preferred by adults. In historically stable or cycling fisheries, mechanisms must exist whereby larvae or juveniles routinely return to areas of adult abundance (fishery grounds). If the species has not evolved a reproductive strategy to effect this on a regular basis, then the stability of the population or fishery cannot be assumed and it will be difficult, if not impossible, to predict recruitment.

### Factors that Determine Survival of Juveniles

Much argument has been advanced that year-class strength is established very early in the life history of a crab species (see Hankin 1985), yet evidence now exists for at least some species that events which affect later life history stages can be of a magnitude to significantly affect recruitment.

The following sections review the literature for crabs that address these points.

### Commerical Data Quality

With crab, extensive data are available only for those king crab and *Chionoecetes* populations which are managed in an active sense, i.e. where it is important to establish an annual biomass estimate of at least male abundance. Fishing quotas have usually been based on data from research surveys and/or analysis of commercial fishery performance (Colgate 1982; Elner 1982) and are usually some predetermined fraction of male abundance to permit an escapement perceived to maximize reproductive potential (North Pacific Fishery Management Council 1982; Elner and Bailey 1986). Two data quality problems exist which make it difficult to establish and interpret variability in year-class strength for the few populations where even a modest data time series exists. Estimating the abundance of year-classes is biased by factors affecting collection of data with trawl or trap gear and by the spatial distribution of the year-classes being commercially exploited. This is a problem particularly if much stock assessment information is obtained from fishery performance data. Only male or nonovigerous

female crabs are predominantly exploited, and estimation of female abundance for most species except red king crab has been generally ignored (e.g. Colgate 1982). This results from some spatial separation of the sexes during much of the year, use of ports to allow escape of sublegal-size crabs (including most females), and variable gear selectivity, because of either size or behaviour, between the sexes.

With *Cancer* and *Callinectes*, fisheries are managed primarily with a minimum size limit in combination with area and season closures. No annual quotas are established, and landings in fully exploited fisheries are determined directly by legal crab abundance. Females may be exploited, but usually not while ovigerous. In these fisheries, few data on female fecundity or abundance are available, as they cannot be obtained from sampling the commercial catch. Few fisheries are sufficiently valuable and/or geographically discrete to justify costly annual resource surveys.

In many fisheries, accuracy of landing statistics may be questionable; unreported landings are often common (Jamieson 1986). Data collection can also bias results. For example, between 1980 and 1981, the procedure for estimating blue crab landings in Maryland was modified to permit random subsampling of the approximately 20 000 license holders. Official landing almost doubled (1980, 12 000 t; 1981, 23 500 t), and it was felt that new assessment procedures may have increased estimated landings by a factor of 1.5–1.8 (C. Bonzek, pers. comm.). The magnitude of this problem probably varies between fisheries and over time and is unquantifiable. It can only be assumed that the best fishery performance data are always being made available, while recognizing that often only trends are being indicated.

## The Parent Population

With extensive larval dispersal being a characteristic of most crab species, it would seem unlikely that a reproductive strategy exists which maximizes survival in each unique environmental situation over a species' range. There is no evidence that crab larvae "home" to the specific location where they were hatched. For Dungeness crab at least, it has been concluded that an extensive pelagic larval stage, which is continuously exposed to strong currents, prevents development of discrete populations (Soulé and Tasto 1983). For example, off central California, zoeae hatch in late winter and are carried northward by the Davidson Current. Late-stage zoeae are found offshore and it seems that megalopae somehow return inshore after the Davidson Current has broken down. There is no data which suggest that megalopae direct their swimming in an easterly direction or that vertical swimming behaviour facilitates return to a specific latitudinal location through use of favourable current patterns. A biological return response appropriate for central California may not necessarily be advantageous in the waters off British Columbia or Alaska, where neither hydrographic regime is similar to that off California (e.g. Freeland et al. 1984; Hickey 1979), and so magnitude of return may depend largely on environmental factors.

The range of Dungeness crab is such that considerable mixing of progeny hatched at different sites likely occurs. It becomes impossible to identify clearly the parent population for any particular fishing location's recruitment, and in many cases, it may be questionable whether the local population regularly contributes substantially to local recruitment. The same situation exists for blue crab, where it is not clear whether recruitment in Chesapeake Bay occurs from larvae retained in the Bay or from those found outside the Bay, and for the latter larvae, what their origin was. Documentation of crab larval dispersal and our understanding of the factors which influence it are incomplete.

Crab populations in which larval distributions have been documented most extensively are Chesapeake Bay blue crab, central California–Oregon Dungeness crab, and southeastern Bering Sea red king and tanner crabs (see Sulkin and Epifanio (1986), Reilly (1983, 1985), and Armstrong et al. (1983) for reviews of each species, respectively).

## Fecundity

To understand the stock–recruitment relationship or to manage with the objective of maximizing reproductive potential, it is critical to establish the characteristics of the female cohort and its production of progeny. For species other than red king crab, it has been assumed that female year-class strength reflects that of the male's, that an apparent lack of barren females indicates that a sufficient number of males are present for female fertilization, and that larval production per female at size remains constant over time. Evidence in support of these three assumptions largely is nonexistent. The first assumption of comparable abundance between the sexes of a given year-class generally might be acceptable although natural mortality may be greater for smaller individuals because of predation or cannibalism. Mature female crab are smaller than mature male crab of the same year-class, and so male abundance may indicate poorly the relative female abundance between year-classes of females. Tasto (1983) observed more males among larger Dungeness crab prerecruits but whether this was the result of sampling design bias or differential size-specific mortality was not determined.

The second assumption of a high fertilization rate is based on limited observations which indicate that most mature females are ovigerous (e.g. Colgate 1982; Elner and Gass 1984; Elner and Bailey 1986). The usual assumption is that the entire female population is being randomly sampled and that the behaviour of ovigerous and nonovigerous female crabs does not differ. For at least edible and blue crabs, this does not appear to be the case (Howard 1982; Van Engel 1958). Ovigerous females congregate in particular locations to incubate their eggs and their behaviour may prevent many of them from entering traps. Few attempts have been made to assess experimentally the effect of varying the sex ratio on reproductive potential, and when it has been done (e.g. Powell et al. 1974), extrapolation to conditions in other years remains a problem (Reeves 1982). Finally, there is evidence in both Dungeness crab and red king crab that effective female fecundity at size differs both between populations and over time. For example the magnitude of abundance of predatory nemerteans in Dungeness crab egg masses varies considerably latitudinally (Wickham 1979a, 1979b), with significant predation of eggs in California but little evidence of significant predation in British Columbia (unpubl. data). Around Kodiak Island, nemerteans have been observed only recently in high abundance on red king crab (D. Wickham, pers. comm.).

The most comprehensive data base on annual crab fecundity is that for Bristol Bay red king crab, which has been monitored since 1968. Management of this fishery is based on a stock–recruitment relationship, the effects of male removal on fertilization, and the determination of quotas based on spawn-

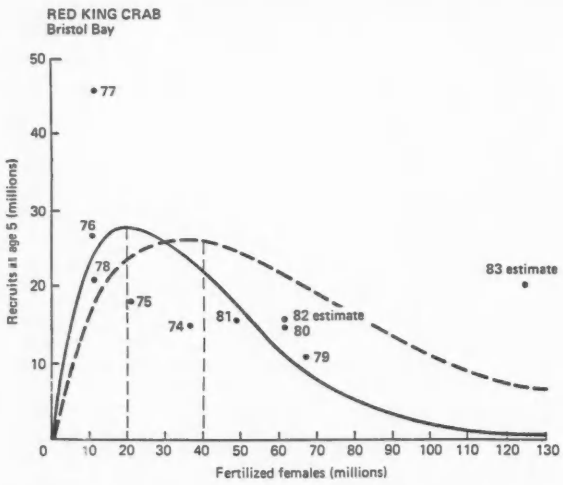


FIG. 7. Spawner–recruit relationships for Bristol Bay red king crab using the 1968–81 survey data (—) and the 1968–81 data plus estimates of recruitment for 1982 and 1983 (---) (from Reeves 1982).

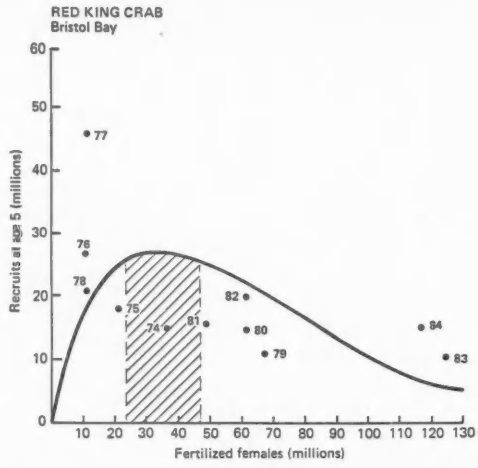


FIG. 8. Spawner–recruit relationship in 1985 for Bristol Bay red king crab. Each point is designated by the year of the recruitment estimate. The shaded area is the threshold region giving the highest probability of strong future male recruitment (from Reeves 1985).

ing stock condition (Reeves 1982). At present, a Ricker-type recruitment model best describes the relationship of progeny (abundance of 5-yr-old males) to that of fertilized females 6 yr earlier (Reeves 1982), and when recruitment estimates for the next 2 yr are included (Fig. 7), a threshold region can be defined which, when occupied by the spawning stock, is assumed to represent the highest probability of strong future male recruitment. This region is currently defined (Reeves 1985) by the 95% confidence interval on the abundance of female spawning producing maximum future recruitment of 5-yr-old males (Fig. 8). Female and prerecruit male cohort strengths are obtained by trawl data from research surveys (e.g. Otto et al. 1984), and maturity schedules, mating characteristics, and clutch size and viability are integral components of the analysis (Reeves 1982).

However, with only 11 yr of data available, much about the population dynamics of this species remains unknown and it appears that relating eggs to recruits alone is not sufficient for satisfactory stock management. Unusually high natural mortality of unknown cause among older prerecruits and females ($M$ was estimated at 2.94 for 5- to 6-yr-old females in 1982–83 (J. E. Reeves, pers. comm.)) has characterized the population in recent years, and this has plunged female and subsequent legal male abundance below predicted levels (Otto 1984). Problems with reduced clutch size also occurred in 1982 (Hayes 19834; Otto et al. 1983), and with high mortality, this has made future abundance and stock status predictions difficult. Resulting management advice has been necessarily conservative (Reeves 1985), and it is apparent that additional studies are required if causes of such fluctuations are to be adequately understood.

## "Critical" Life Stages

Reilly (1983, 1985) uses the term "critical" life stage (May 1974) as one in which a year-class suffers sufficient mortality or displacement to determine year-class strength in terms of future fishery performance. From 1975 through 1980, a comprehensive study was conducted by the California Department of Fish and Game in the Gulf of Farallones and San Francisco – San Pablo – Suisun Bay complex to determine if there was any consistency in critical life stage in these Dungeness crab populations (Wild and Tasto 1983). No consistent relationship between relative abundances of stage I zoeae and megalopae of the same year-class could be found. A direct relationship between abundance of stage I zoeae, megalopae, and the resulting juvenile year-class was found in 1978 and 1979, but in 1976, zoeal abundance was high but megalopae and resulting juvenile abundance in both the Gulf and Bay were low (Reilly 1983, 1985). Relationships in other years are not referred to, and are assumed to be ambiguous. The most consistent relationship observed was that relative abundance of megalopae was directly related to abundance of first instar crabs of that year-class.

While the above comprehensive study failed to clearly establish a relationship between larval abundance and subsequent recruitment to the commercial fishery for a given year-class, it does serve to emphasize the significant logistic difficulties in assessing a stock–recruitment relationship when both ultimate destinations of locally produced larvae and origins of settling megalopae are unknown. A greater understanding of oceanography and species behaviour and ecology would seem to be required if survey results to estimate relative abundances of various life stages are to be satisfactorily interpreted.

The hypothesis that year-class strength is established during the early life stages of a species (see May 1974) has been advocated by many authors studying crab (Hankin 1985; McKelvey et al. 1980; Reilly 1983, 1985; Sulkin and Van Heukelem 1982; Wickham 1979a), using often very different arguments. However, it has also been proposed that predation (including cannibalism) of juvenile crab can determine year-class strength (Armstrong and Gunderson 1985; Bailey 1982; Botsford and Wickham 1978; Peterson 1973; Waiwood and Elner 1982), again using often very different arguments. Unusually high mortalities experienced by large prerecruit crab in the eastern Bering Sea in the early 1980's (Hayes 1983; R. Otto, pers. comm.) confirm that while of unknown origin,

TABLE 1. Coefficients of variation for annual fluctuation of commercial landings for selected crab fisheries.

| Fishery | Time period | No. of years | Annual landings (t) Mean | SD | CV(%) |
|---|---|---|---|---|---|
| Edible crab[a] | 1964–83 | 20 | | | |
| Norway | | | 2 600 | 570 | 22 |
| Scotland | | | 2 300 | 550 | 24 |
| England | | | 4 826 | 1 750 | 36 |
| France[b] | | | 3 133 | 1 276 | 41 |
| Blue crab[c] | 1965–84 | 20 | | | |
| Middle Atlantic | | | 2 103 | 2 012 | 96 |
| Chesapeake Bay | | | 54 302 | 19 998 | 37 |
| South Atlantic | | | 33 869 | 6 294 | 19 |
| Dungeness crab | | | | | |
| British Columbia | 1963–82 | 20 | 1 396 | 445 | 32 |
| Washington[d] | 1964–65 to 1983–84 | 20 | 3 691 | 2 036 | 55 |
| Oregon[e] | 1964–65 to 1983–84 | 20 | 4 353 | 2 110 | 48 |
| Northern California[f] | 1964–65 to 1983–84 | 20 | 3 943 | 2 695 | 68 |

Data sources:

[a]FAO Yearbooks Fishery Statistics, Vol. 22.
[b]D. Latrouite (pers. comm.).
[c]NMFS Statistics Digest, 1951–76; state and federal fisheries personnel, pers. comm., 1977–84.
[d]Barry (1985), coastal waters only.
[e]D. Demory (pers. comm.).
[f]Warner (1985).

mortality of late-stage prerecruits can be significant and cause fishery decline. All crab life stages are thus potentially critical, and while one life stage may appear to be more critical than the others for a given population in a given year, there is no evidence to suggest that this will consistently be the case in future years or apply to different populations.

## Annual Variability

All fisheries characteristically fluctuate in abundance, but it is the magnitude of fluctuation which is of particular importance. For many fisheries, these fluctuations seem relatively modest, with average annual coefficients of variation of <35% (Table 1). The relatively recent establishment of some fisheries and the resulting short time series of data of an expanding fishery nature (e.g. *Chionoecetes*) have made the evaluation of fluctuation magnitude sometimes difficult. However, for fisheries not at the edge of a species' distribution and which have been exploited for decades, such as Dungeness crab in British Columbia, edible crab in England, and blue crab in Chesapeake Bay, most fluctuations in landings have generally been modest. Landings from individual subfisheries may fluctuate more, as shown by individual landings from eight identified fishing areas in British Columbia (Jamieson 1985, fig. 3), but for most large geographic areas (e.g. British Columbia (Fig. 4)), overall landings have been relatively stable.

With the generally poor quality of data, if any pattern exists, it is that populations at the periphery of the range of distribution of a species seem to fluctuate most. Thus, in species with predominantly a north–south distribution and in which fisheries are fully developed, fluctuations of the greatest magnitude have occurred in northern California for Dungeness crab (Fig. 4), in Brittany for edible crab (Fig. 5), and in the Middle Atlantic (New York, New Jersey, and Delaware) statistical area for blue crab (Fig. 6). No comparable pattern is as evident in red king crab or in *Chionoecetes*, perhaps because adjacent fisheries for such species are largely at the same latitude. Biologically, this is not surprising, as one would expect that on the periphery of a species' distribution, recruitment magnitude might be more affected by the fortuitous occurrence of favourable circumstances and be less likely to be established in a general state of equilibrium.

The pattern of fluctuation of landings in some crab fisheries suggests that fluctuations may be cyclical, but with a maximum data time series only of about 30 yr and with suggested cycles of about 9–15 yr, generally insufficient data are available for any definitive conclusions to be drawn. Whether a population really is cycling in abundance, and if so, what are the mechanisms which may be driving it are both questions that in general have not been resolved at this time for most fisheries.

The best time series of cycling abundance in a crab population is that for northern California Dungeness crab, which shows evidence of three cycles in abundance since 1954 (Fig. 4). Bristol Bay red king crab landings suggest two recent cycles in abundance (Fig. 1), but when this is compared with estimated annual abundances of fertilized females (J. E. Reeves, unpubl. data), the pattern becomes less clear. Since 1968, female abundance was reasonably high between 1973 and 1981, with a period of very high abundance between the years 1977 and 1979 (Fig. 9). In contrast, legal male abundance increased each year from 1972 to 1978. Part of the problem in interpreting these data is that both annual commercial landings of males and estimates of female abundance involve a number of year-classes, legal-size males are older than the age at which females of the same year-class can first be fertilized (a time lag therefore exists), and that with only 11 yr of data available, the data series is short.

However, consideration of these data does suggest an additional interesting point. The reason for the apparently good Ricker stock–recruitment relationship suggested for this species is that when female abundance was low, resulting recruitment of progeny (5-yr-old males) was high, and that when

female abundance was relatively high, recruitment was low (Fig. 9). However, because of the 6-yr time lag between female abundance and recruitment of 5-yr-old males, and the possibly cyclic nature of abundance in this species, this relationship may well be an artifact. It could well be that survival of sublegal-size crab, male or female, was favoured in the mid-1970's, but has not been in recent years. This would generate the same pattern of response but would imply no stock–recruitment relationship.

On purely theoretical grounds, it is hard to deny a stock–recruitment relationshp at low stock levels, and while the rationale for the Alaskan management approach is based on this premise, the real problem may be in defining exactly what is meant by "low." It may be a population level well below that which can support a substantial fishery.

## Causative Hypotheses for Recruitment Fluctuation

Studies to identify and document the causative elements behind fluctuations in year-class strength have been of two types: (1) empirical study of life stages in the field, and by monitoring the occurrence and abundance of different life stages, evaluation of reproduction and potential influencing factors (e.g. Epifanio et al. 1984; Lough 1976; McConaugha et al. 1983; Smyth 1980; Sulkin and Epifanio 1986; Wild and Tasto 1983 and references therein), and (2) the theoretical discussion and analysis of mechanisms which might affect recruitment and/or the subsequent testing and verification of hypotheses (e.g. Botsford et al. 1983; Botsford 1984; McKelvey et al. 1980; Peterson 1973; Johnson et al. 1984; Sulkin et al. 1980). The empirical data have already been discussed, and while basic patterns of larval dispersal and their subsequent return to locations of juvenile and/or adult survival have been described for at least some populations, factors affecting the magnitude of both return and survival are still largely hypothetical. In this section of the paper, such hypotheses will be briefly reviewed and discussed, with particular emphasis on Dungeness and blue crabs because of the relatively extensive literature on these species.

A number of scientists have proposed hypotheses to explain cyclic fluctuations in magnitude of northern California Dungeness crab landings, and opposing perspectives, notably between L. Botsford and D. Hankin, have led to one of the more interesting, ongoing scientific exchanges in the recent published literature. Three broad categories of mechanisms have been reviewed by Armstrong (1983), Botsford (1986), and Hankin (1985) as the causes of cycles in northern California Dungeness crab: (1) predator–prey interactions, (2) density-dependent recruitment, and (3) cyclic environment variables.

In the first category, two potential predators, man through fishing (Botsford et al. 1983) and salmon [chinook (king), *Oncorhynchus tshawytscha,* and coho (silver), *O. kisutch*] through predation on megalopae (Botsford et al. 1982) have been discounted. In the former, the required lag between a decline in fishing effort and the subsequent increase in crab abundance was not evident. In the later, although salmon and crab landings were cyclic with the same period, the phase relationship implied by larval predation did not match the lags observed. Data are largely insufficient for investigation of other likely predator–prey senarios in northern California, and so this causal mechanism cannot be pursued much further.

Thomas (1986) has suggested that coho, particularly those reared in hatcheries, may be the major limiter of crab megalopae survival in central California, and the reason why crab landings failed to recover from a coastwide low during the early 1960s. However, his evidence is circumstantial and further analysis and study is needed before his hypothesis can be supported.

The second category, density-dependent recruitment, has been studied by developing mathematical population models, determining the conditions necessary to cause cycles in these models, and then testing proposed mechanisms against these conditions. Three density-dependent mechanisms have been hypothesized: egg predation by a worm (Wickham 1979a), juvenile cannibalism by older crabs (Botsford and Wickham 1978), and egg/larval survival mediated through fluctuations in total egg production by the unexploited female population (McKelvey et al. 1980). Philosophical differences between individuals as to what criteria warrant rejection of hypotheses confuse the evaluation of these mechanisms, but it is generally agreed (Botsford 1986; Hankin 1985) that the egg – predator worm can be discounted as the sole cause. Crab survival with increasing worm population size by itself does not decrease rapidly enough to destabilize the population and cause cycles (Botsford 1986). Density-dependent natality and subsequent larval survival remains a possible causal mechanism, although whether such a mechanism actually exists is unclear, since there are no biological data to support it. The cannibalism hypothesis is a complex issue which is still being actively debated, with no likely consensus until more empirical data have been obtained.

Mechanisms in the third category have been evaluated by computing correlations between environmental factors and commercial landings or larval abundance. Mechanisms include upwelling and its effect on food availability (Peterson 1973), sea temperature and the possible deleterious effect of warmer water on egg development (Wild 1980), sunspot activity and an unknown biological connection (Love and Westphal 1983), and spring wind stress and its influence on the return of megalopae to shore (Botsford 1986). There is a general consensus that upwelling and sunspot activity do not satisfy criteria for being the cause of observed cycles (Botsford and Wickham 1975; Botsford 1986; Hankin 1985). It could not be shown that upwelling was driving the cycles in the sense that cycles in catch were following cycles in upwelling, and the lack of a biological basis behind sunspot activity makes this mechanism questionable. Again, because of differences of opinion in rejection criteria, no consensus on the influence of sea temperature exists. The spring wind stress mechanism has not yet been described sufficiently in the literature and is still being analysed (L. W. Botsford, pers. comm.).

No single factor alone seems sufficient to explain recruitment variation in Dungeness crab (Armstrong 1983; Botsford 1986; Hankin 1985), and interaction between density-dependent and environmental forcing hypotheses is now being advocated. The main consensus is that additional biological study in the field is needed if resolution of causative mechanisms is to be achieved. There is currently a lack of appropriate data of acceptable quality to resolve hypothesized issues.

In blue crab, density-dependent mortality is recognized but its relative significance in influencing recent annual variation in crab year-class strength in Chesapeake Bay is unknown. Most recent studies have focused on the influence of shelf water

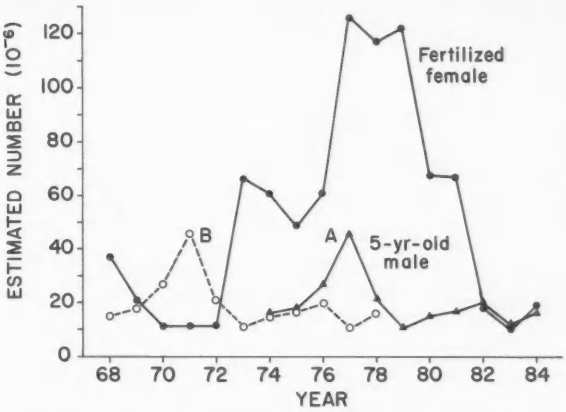


FIG. 9. Estimated annual numbers of fertilized females (●) and 5-yr-old male red king crab in Bristol Bay, Bering Sea. A, actual years in which prerecruit male crabs (▲) were observed; B, 6-yr lag removed to show comparison of prerecruit male abundance (○) with female parent abundance by year. Data were obtained from National Marine Fishery Service surveys and are those used to estimate spawner–recruit parameters (modified from Reeves 1985).

circulation on the degree of retention of larvae rather than factors affecting level of overall larval production. On the basis of theoretical arguments, it has been suggested that the former most influences annual reproduction to the juvenile stage, within limits imposed by density-dependent mortality (Sulkin and Epifanio 1986). Transport of megalopae approaching metamorphosis by deeper shelf water exhibiting a shorewood residual drift was hypothesized by Sulkin and Epifanio (1986), while Johnson et al. (1984) hypothesized a northward surface water counterflow generated by wind stress as a mechanism which reduces the chance that larvae are being advected south and lost from the area of Chesapeake Bay. The dominant mechanism for onshore transport of pelagic stages remains unknown, but it likely involves both active (crab behaviour) and passive (environmental) processes. As a result, it has been suggested that neither estimates of spawning stock size nor larval abundance on the shelf are likely to provide useful predictive information on year-class strength at recruitment (Sulkin and Epifanio 1986). Monitoring of early juvenile abundance is the only suggested reliable procedure.

## Resource Management Implications

It is evident from the above that for most crab populations, (1) little information on the causes or patterns of annual variability is available, (2) management seems to have had no demonstrated effect on the magnitude or incidence of fluctuations, and (3) present crab management has often been structured in a way that does not require advance prediction of future fluctuations in population abundance. This latter point is perhaps a "chicken-or-egg" scenario, but it is also a function of the way in which different crab fisheries (shallow versus deep water) have developed.

Extensive crab fisheries first developed in the late 1800's and were focused on nearshore, shallow-water species such as *Cancer edulis*, *C. magister* and *Callinectes sapidus*. These crabs could be fished by hand-operated gear from small boats, and because of crab habitat preferences, areas of abundance were readily identifiable. As discussed by Jamieson (1986), the geographically widespread distribution of fishing effort, relatively small landings at any locality, and limited enforcement and research resources all favoured development of passive management, which involves no annual regulation of landings in response to crab abundance and only occasional local area and/or seasonal closures and a minimum legal size limit. Once entrenched, this management system has persisted to the present. It requires no advance prediction of significant fluctuations in crab anbundance, and history has shown that with traditional levels of effort, the economic fortunes of participating fishermen are seldom unduly compromised. Fluctuations in abundance have encouraged involvement of crab fishermen in other fisheries, or vice versa, since such involvement (Jamieson 1985) seems to stabilize cash flow.

The challenge today is that because numbers of fishermen have typically increased over time in most fisheries, while the abundance of crab has not, crab fishing has become particularly competitive and often overcapitalized. Advance knowledge of major fluctuations in abundance can lead, in theory at least, to more efficient utilization of available fishing units and so optimize benefits to society. This has stimulated interest by scientists and resource managers in ascertaining if crab yields over the long term can be increased, or at least better utilized.

It is thus perhaps no coincidence that the greatest interest in understanding fluctuations in abundance of shallow-water crab species by managers and funding agencies has been directed towards those populations of a given species which have historically fluctuated the most. These are usually at the periphery of the range of distribution of a species, and while the study of population dynamics of such resources might most likely demonstrate significant interaction with potential causative variables, observations may be particularly time or site specific. Recruitment in abundance at the fringe of a species' distribution may be often determined by a fortuitous event (e.g. El Niño, a severe storm, etc.). In contrast, in the central part of a species' range, where the species may be more physiologically and behaviourally adapted to environmental conditions, magnitude of recruitment fluctuation seems often to be less and recruitment would likely be influenced by the synergistic interactions of a relatively large number of perhaps more minor variables. Under such circumstances, management concern and research priority would be lessened and priority would tend to be given to other fisheries.

This has been unfortunate, since detailed study of a species throughout its range is needed to obtain a fundamental understanding of factors affecting year-class strength. Our recent history of studying only a few, perhaps unique, populations delineated by political boundaries rather than biological ones is a poor second alternative. In this respect, an attempt is being made to develop a multiyear study of Dungeness crab from California north to at least British Columbia, with the intent of documenting larval dispersal and settlement patterns in the broad sense. Such a coordinated study is required if the larval dynamics of this species are ever to be satisfactorily understood.

An alternative development scenario exists with offshore, deeper-water crab fisheries. Exploitation of these species is capital intensive and requires large vessels and gear and, because these fisheries are often geographically remote from markets, the use of sophisticated freezing or live-holding facilities. As a result, exploitation has depended on recent advances in

technology and has been intensive only in the last few decades. The combination of high fishery value, recent advances in fishery management and stock assessment theory, and a perceived need and ability to control major resource utilization has resulted in active management (annual regulation of landings in response to crab abundance) of these fisheries almost from their onset. These fisheries have the greatest perceived, immediate need for timely and accurate forecasting of fluctuations in abundance. Capital investment is substantial and the harvest of alternate, unexploited resources is needed if crabs alone do not allow profitable fishing.

The two fisheries that best typify the above are Alaskan king and tanner crab exploitation, which largely involves only one fleet in a given management area, and snow crab exploitation in Atlantic Canada. As indicated earlier, although king crab have been intensively managed since 1968 with a policy to establish stability and eliminate, as much as possible, extreme fluctuations in harvest yield (Alaska Department of Fish and Game, 1983 Commercial Shellfish Regulations), red king crab populations have nevertheless declined significantly and the fishery has collapsed. Biological advice was largely followed and no obvious mistakes were made, indicating that, relative to environmental factors, control of red king crab recruitment through management of adult abundance appears slight.

Snow crab have been exploited fully for less than a decade, and so natural, major fluctuations in population abundance perhaps are not yet evident. However, the recent substantial decline in landings in Newfoundland may indicate the beginning of a period of low abundance. Quotas are set somewhat arbitrarily and have been about 50–60% of estimated legal male biomass (Elner 1982), but again, in the absence of experimental fishing, the impact of the fishery on the stock cannot be determined.

One will never know if overall yield over time has been enhanced because of past management of crab resources. It would seem that the greatest benefit of active management may have been that by establishing clear procedures for exploitation, crab resources have been harvested in a coordinated, generally efficient, socially acceptable manner. The importance of this benefit should not be underestimated, since this objective is assuming an ever larger proportion of management rationale in an increasingly complex industry. Management of a "fishery" often involves more time and funds than management of the resource per se, and social and economic considerations alone are often justified as the basis for management action. This should not imply that resource and oceanographic monitoring or the modelling of crab population dynamics presently being undertaken should be curtailed or terminated, since in the future, the effects of resource management should become more apparent and more successful prediction of fluctuations in abundance may be possible. However, experience to date suggests that this may take decades and that scientists, managers, research funding agencies, fishermen, and other interested parties should realize this clearly and plan accordingly. Until we better understand ocean climate and crab biology, we will not be able to manipulate or predict crab resource abundance to desired standards. Stock abundances will continue to fluctuate substantially and fishing will remain the dynamic enterprise that it is.

## References


ADAMS, A. E. 1979. The life history of the snow crab, *Chionoecetes opilio*: a literature review, Mar. 1979, Alaska Sea Grant Rep. 78-13: 141 p.

ARMSTRONG, D. A. 1983. Cyclic crab abundance and relationship to environmental causes, p. 102–110. *In* W. S. Wooster [ed.] From year to year: interannual variability of the environment and fisheries of the Gulf of Alaska and the eastern Bering Sea, Oct. 1983. Washington Sea Grant Publ. WSG-WO 83-7.

ARMSTRONG, D. A., AND D. R. GUNDERSON. 1985. The role of estuaries in Dungeness crab early life history: a case study of Greys Harbour, Washington. Proc. Symp. Dungeness Crab Biology and Management, April 1985. Alaska Sea Grant Rep. 85-3: 145–170.

ARMSTRONG, D. A., L. S. INCZE, D. L. WENCKER, AND J. L. ARMSTRONG. 1983. Distribution and abundance of decapod crustacean larvae in the southeastern Bering Sea with emphasis on commercial species. Final Rep. to OCSEAP–Office of Marine Pollution Assessment NA81-RAC-00059, RU-609: 373 p.

BAILEY, R. 1982. Relationship between catches of snow crab, *C. opilio* (*O. fabricius*) and abundance of cod (*Gadus morhua* L.) in the southwestern Gulf of St. Lawrence. Proc. Int. Symp. Genus *Chionocetes*, Univ. Alaska, Dec. 1982. Alaska Sea Grant Rep. 85-3: 485–497.

BARRY, S. 1985. Overview of the Washington coastal Dungeness crab fishery. Proc. Symp. Dungeness Crab Biology and Management, April 1985. Alaska Sea Grant Rep. 85-3: 33–36.

BLAU, S. F. 1986. Recent declines of red king crab (*Paralithodes camtschatica*) populations and reproductive conditions around the Kodiak Archipelago, Alaska, p. 360–369. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

BOTSFORD, L. W. 1984. Effect of individual growth rates on expected behaviour of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 41: 99–107.

1986. Population dynamics of the Dungeness crab (*Cancer magister*), p. 140–153. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

BOTSFORD, L. W., R. D. METHOT JR., AND W. E. JOHNSTON. 1983. Effort dynamics of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 40: 337–346.

BOTSFORD, L. W., R. D. METHOT, AND J. E. WILEN. 1982. Cyclic covariation in the California king salmon, *Oncorhynchus tshawytscha*, silver salmon, *O. kisutch*, and Dungeness crab, *Cancer magister*, fisheries. Fish. Bull. U.S. 80: 791–801.

BOTSFORD, L. W., AND D. E. WICKHAM. 1975. Correlation of upwelling index and Dungeness crab catch. Fish. Bull. U.S. 73: 901–907.

1978. Behaviour of age-specific and density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35: 833–843.

BROWN, C. G., AND D. G. BENNETT. 1980. Population and catch structure of the edible crab (*Cancer pagurus*) in the English Channel. J. Cons. Int. Explor. Mer 39(1): 88–100.

COLGATE, W. A. 1982. A review of the Gulf of Alaska tanner crab, *Chionoecetes bairdi*, fishery and management related research. Proc. Int. Symp. Genus *Chionoecetes*, Univ. Alaska, Dec. 1982. Alaska Sea Grant Rep. 85-3: 41–70.

EATON, M. F. 1985. Kodiak Island commercial Dungeness, *Cancer magister*, fishery. Proc. Symp. Dungeness Crab Biology and Management, April 1985. Alaska Sea Grant Rep. 85-3: 97–118.

EDWARDS, E. 1979. The edible crab and its fishery in British waters. Fishing News Books Ltd., Farnham, England. 140 p.

ELNER, R. W. 1982. Overview of the snow crab *Chionoecetes opilio* fishery in Atlantic Canada. Proc. Int. Symp. Genus *Chionoecetes*, Dec. 1982. Alaska Sea Grant Rep. 82-10: 3–20.

ELNER, R. W., AND R. F. J. BAILEY. 1986. Differential susceptibility of Atlantic snow crab, *Chionoecetes opilio*, stocks to management, p. 335–346. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

ELNER, R. W., AND C. A. GASS. 1984. Observations on the reproductive condition of female snow crabs from NW Cape Breton Island, November 1983. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 84/14: 19 p.

EPIFANIO, C. E., C. C. VALENTI, AND A. E. PEMBROKE. 1984. Dispersal and recruitment of blue crab larvae in Delaware Bay, U.S.A. Estuarine Coastal Shelf Sci. 18: 1–12.

FREELAND, H. J., W. R. CRAWFORD, AND R. E. THOMSON. 1984. Currents along the Pacific coast of Canada. Atmosphere-Ocean 22: 151–172.

HANKIN, D. G. 1985. Proposed explanations for fluctuations in abundance of Dungeness crabs: a review and critique. Proc. Symp. Dungeness Crab Biology and Management, April 1985. Alaska Sea Grant Rep. 85-3: 305–326.

HART, J. F. L. 1982. Crabs and their relatives of British Columbia. B.C. Prov. Mus. Handb. 40: 266 p.

HAYES, M. L. 1983. Variation in the abundance of crab and shrimp with some hypotheses on its relationship to environmental causes, p. 86–100. *In* W. S. Wooster [ed.] From year to year: interannual variability of the environment and fisheries of the Gulf of Alaska and the eastern Bering Sea, Oct. 1983. Washington Sea Grant Publ. WSG-WO 83-7.

HAYNES, E. B. 1974. Distribution and relative abundance of larvae of king crab, *Paralithodes camtschatica*, in the southeastern Bering Sea, 1969–70. Fish. Bull. U.S. 72: 804–812.

HEBARD, J. G. 1959. Currents in southeastern Bering Sea and possible effects upon king crab larvae. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 293: 11 p.

HESTER, B. S. 1983. A model of the population dynamics of the blue crab in Chesapeake Bay (Maryland, Virginia). Ph.D. thesis, Old Dominion University, Norfolk, VA. 150 p.

HICKEY, B. M. 1979. The California Current system — hypotheses and facts. Prog. Oceanogr. 8: 191–279.

HOWARD, A. E. 1982. The distribution and behaviour of ovigerous, edible crabs (*Cancer pagurus*), and consequent sampling bias. J. Cons. Int. Explor. Mer 40: 259–261.

JAMIESON, G. S. 1985. The Dungeness crab, *Cancer magister*, fisheries of British Columbia. Proc. Symp. Dungeness Crab Biology and Management, April 1985. Alaska Sea Grant Rep. 85-3: 37–60.

1986. A perspective on invertebrate fisheries management – the British Columbia experience, p. 57–74. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

JAMIESON, G. S., AND N. A. SLOAN. 1985. King crabs in British Columbia. Proc. of the Int. King Crab Symp., January 22–24, 1985, Anchorage, Alaska. Alaska Sea Grant Rep. 85-12: 49–62.

JOHNSON, D. F. 1982. A comparison of recruitment strategies among brachyuran crustacean megalopae of the York River, lower Chesapeake Bay and adjacent shelf waters. Ph.D. thesis, Old Dominion University, Norfolk, VA. 97 p.

JOHNSON, D. F., B. S. HESTER, AND J. R. MCCONAUGHA. 1984. Studies of a wind mechanism influencing the recruitment of blue crabs in the Middle Atlantic bight. Continental Shelf Res. 3: 425–437.

KOENEMAN, T. M. 1985. A brief review of the commercial fisheries for *Cancer magister* in southeast Alaska and Yakutat waters, with emphasis on recent seasons. Proc. Symp. Dungeness Crab Biology and Management, April 1985. Alaska Sea Grant Rep. 85-3: 61–76.

LOUGH, R. G. 1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970–71. Fish. Bull. U.S. 74: 353–375.

LOVE, M. S., AND W. V. WESTPHAL. 1983. A correlation between annual catches of Dungeness crab, *Cancer magister*, and mean annual sunspot number. Fish. Bull. U.S. 79: 794–795.

MAY, R. C. 1974. Larval mortality in marine fishes and the critical period concept, p. 3–19. *In* J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York, NY.

MCCONAUGHA, J. R., D. F. JOHNSON, A. J. PROVENZANO, AND R. C. MARIS. 1983. Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea: Decapoda) in the waters adjacent to Chesapeake Bay. J. Crustacean Biol. 3: 582–591.

MCKELVEY, R., D. HANKIN, R. YANOSKO, AND C. SNYGG. 1980. Stable cycles in multistage recruitment models: an application to the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37: 2323–2345.

METHOT, R. D. JR., AND L. W. BOTSFORD. 1982. Estimated preseason abundance in the California Dungeness crab (*Cancer magister*) fisheries. Can. J. Fish. Aquat. Sci. 39: 1077–1083.

NORSE, E. A. 1977. Aspects of the zoogeographic distribution of *Callinectes* (Brachyura: Portunidae). Bull. Mar. Sci. 27(3): 440–447.

NORTH PACIFIC FISHERY MANAGEMENT COUNCIL. 1982. Bering Sea/Aleutian Islands king crab fishery management plan. North Pacific Fishery Management Council, P.O. Box 3136 DT, Anchorage, AK 99510. 102 p.

OTTO, R. S. 1981. Eastern Bering Sea crab fisheries, p. 1037–1066. *In* D. W. Hood and J. A. Calder [ed.] The eastern Bering Sea Shelf: oceanography and resources. Vol. 2. University of Washington Press, Seattle, WA.

1982. An overview of the eastern Bering Sea tanner crab fisheries. Proc. Int. Symp. Genus *Chionoecetes*, Dec. 1982. Alaska Sea Grant Rep. 82-10: 83–118.

1984. Egg production and Bristol Bay red king crab 1979–1983. Report to North Pacific Fish. Management Council and the Alaska Board Fish., Anchorage, Alaska, March 26–30, 1984. Natl. Mar. Fish. Serv., Kodiak Facility, P.O. Box 1638, Kodiak, AK. 5 p. (Mimeo.)

OTTO, R. S., R. A. MACINTOSH, AND W. S. MEYERS. 1983. Current status of reproductive conditions in Bristol Bay red king crab. Report to North Pacific Fish. Management Council and the Alaska Board Fish., Anchorage, Alaska, March 29–30, 1983. Natl. Mar. Fish. Serv., Kodiak Facility, P.O. Box 1638, Kodiak, AK. 14 p. (Mimeo.)

OTTO, R. S., B. G. STEVENS, R. A. MACINTOSH, K. L. STAHL-JOHNSON, AND S. J. WILSON. 1984. United States crab research in the eastern Bering Sea during 1984. (Document submitted to the annual meeting of INPFC, October 1984). Northwest and Alaska Fisheries Center, Natl. Mar. Fish. Serv., NOAA. 39 p.

PERRY, H. M. 1975. The blue crab fishery in Mississippi. Gulf Res. Rep. 5: 39–57.

PETERSON, W. T. 1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull. U.S. 71: 902–910.

POWELL, G. C., K. E. JAMES, AND C. L. HURD. 1974. Ability of male king crab, *Paralithodes camtschatica*, to mate repeatedly, Kodiak, Alaska, 1973. Fish. Bull. U.S. 72: 171–179.

REILLY, P. N. 1983. Dynamics of Dungeness crab, *Cancer magister*, larvae off central and northern California, p. 57–74. *In* R. W. Wild and R. N. Tasto [ed.] Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Calif. Dep. Fish Game Fish. Bull. 1972.

1985. Dynamics of Dungeness crab, *Cancer magister*, larvae off central and northern California. Proc. Symp. Dungeness Crab Biology and Management, April 1985. Alaska Sea Grant Rep. 85-3: 245–272.

REEVES, J. E. 1982. Data requirements for tanner crab management, as suggested by the Bristol Bay king crab management model. Proc. Int. Symp. Genus *Chionoecetes*, Univ. Alaska, Dec. 1982. Alaska Sea Grant Rep. 85-3: 679–716.

1985. Expected stock status and catch for Bristol Bay red king crab in 1985. Report to North Pacific Fish. Management Council. Natl. Mar. Fish. Serv., NW Alaska Fish. Center, 7600 Sand Pt. Way NE, Bldg. 4, Bin C 15700, Seattle, WA. 9 p. (Mimeo.)

SMYTH, P. O. 1980. *Callinectes* (Decapoda: Portanidae) larvae in the middle Atlantic Bight, 1975–77. Fish. Bull. 78: 251–265.

SOMERTON, D. A. 1981. Life history and population dynamics of two species of tanner crab, *Chionoecetes bairdi* and *C. opilio*, in the eastern Bering Sea with implications for the management of the commercial harvest. Ph.D. thesis, University of Washington, Seattle, WA. 220 p.

SOULÉ, M., AND R. N. TASTO. 1983. Stock identification studies on the Dungeness crab, *Cancer magister*, p. 39–42. *In* R. W. Wild and R. N. Tasto [ed.] Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California Fishery resource. Calif. Dep. Fish Game Fish. Bull. 172.

SULKIN, S. D., AND C. E. EPIFANIO. 1986. A conceptual model for recruitment of the blue crab, *Callinectes sapidus* Rathbun, to estuaries of the Middle Atlantic Bight, p. 117–123. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

SULKIN, S. D. AND W. VAN HEUKELEM. 1982. Larval recruitment in the crab *Callinectes sapidus* Rathbun: an amendment to the concept of larval retention in estuaries, p. 459–475. *In* V. Kennedy [ed.] Estuarine comparisons. Academic Press, New York, NY.

SULKIN, S. D., W. VAN HEUKELEM, AND P. KELLY. 1980. Near-shore larval assemblages as a source of recruitment for estuarine and deeper sea invertebrates. ICES/C.M. 1980/L:58: 15 p.

TASTO, R. N. 1983. Juvenile Dungeness crab, *Cancer magister*, studies in the San Francisco Bay area, p. 135–154. *In* R. W. Wild and R. N. Tasto [ed.] Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California Fishery resource. Calif. Dep. Fish Game Fish. Bull. 172.

TAYLOR, D. M., R. G. HOOPER, AND G. P. ENNIS. 1984. Biological aspects of the spring breeding migration of snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland (Canada). Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 84/58: 11 p.

THOMAS, D. H. 1986. A possible link between coho (silver) salmon enhancement and a decline in central California Dungeness crab abundance. Fish. Bull. 83: 682–691.

VAN ENGEL, W. A. 1958. The blue crab and its fishery in Chesapeake Bay. Part 1 — Reproduction, early development, growth and migration. Comm. Fish. Rev. 20: 6–17.

WAIWOOD, K. G., AND R. W. ELNER. 1982. Cod predation of snow crab (*Chionoecetes opilio*) in the Gulf of St. Lawrence. Proc. Int. Symp. Genus *Chionoecetes*, Univ. Alaska, Dec. 1982. Alaska Sea Grant Rep. 85-3: 499–520.

WARNER, R. W. 1985. Overview of the California Dungeness crab, *Cancer magister*, fisheries. Proc. Symp. Dungeness Crab Biology and Management, April 1985. Alaska Sea Grant Rep. 85-3: 11–25.

WEBER, D. D. 1967. Growth of the immature king crab *Paralithodes camtschatica* (Tilesius). Int. North Pac. Fish. Comm. Bull. 21: 21–53.

WICKHAM, D. E. 1979a. Predation by the nemertean *Carcinonemertes errans* on eggs of the Dungeness crab *Cancer magister*. Mar. Biol. 55: 45–53.

1979b. *Carcinonemertes errans* and the fouling and mortality of eggs of the Dungeness crab, *Cancer magister*. J. Fish. Res. Board Can. 36: 1319–1324.

WILD, P. W. 1980. Effects of seawater temperature on spawning, egg development, hatch success and population fluctuations of the Dungeness crab, *Cancer magister*. Calif. Coop. Oceanic Fish. Invest. Rep. 21: 115–120.

1983. Dungeness crab environment project studies: objectives and approach, p. 171–174. *In* R. W. Wild and R. N. Tasto [ed.] Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California Fishery resource. Calif. Dep. Fish Game Fish. Bull. 172.

WILD, P. W., AND R. N. TASTO [ED.] 1983. Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California Fishery resource. Calif. Dep. Fish Game Fish. Bull. 172: 352 p.

# Problems and Perspectives Regarding Recruitment of Spiny Lobsters, *Panulirus argus*, to the South Florida Fishery

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Inappropriate minimum size, illegal harvest, fishery-induced juvenile growth retardation and mortality, and excessive effort have reduced reproductive contributions and depressed yield-per-recruit in the overcapitalized south Florida spiny lobster (*Panulirus argus*) fishery. Measures recommended to improve yield-per-recruit are as follows: increase minimum legal size to 85–90 mm carapace length; require escape gaps in traps; eliminate possession of sublegal lobsters aboard vessels; prohibit harvest in nurseries; reduce fishing effort; improve enforcement of fishery regulations; and initiate programs to educate fishermen regarding impacts of fishery practices. International management is recommended to assure larval recruitment among Pan-Caribbean stocks.

Dans le sud de la Floride, la pêcherie de la langouste *Panulirus argus*, où sévit déjà la surcapitalisation, souffre des problèmes suivants : taille minimum inadéquate, captures illégales, retards de croissance et mortalité des juvéniles causés par la pêche et effort excessif, qui ont réduit l'apport des reproducteurs et affaibli la production par recrue. Les mesures recommandées pour améliorer la production par recrue sont les suivantes : augmenter la taille légale minimum pour la faire passer de 85 à 90 mm de longueur de la carapace; imposer la présence d'orifices d'échappement dans les casiers; interdire la possession de langoustes de taille inférieure à la norme à bord des bateaux; interdire la capture dans les nurseries; réduire l'effort de pêche; améliorer l'application de la réglementation; enfin, lancer des programmes d'éducation des pêcheurs sur les effets de leurs pratiques. Il est recommandé d'avoir recours à une gestion internationale pour assurer le recrutement des larves parmi l'ensemble des stocks de la mer des Caraïbes.

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Management of the spiny lobster (*Panulirus argus*) resource of south Florida is complicated by uncertainty regarding stock origins and by impacts to stock engendered by excessive harvest competition in the overcapitalized fishery (Gulf of Mexico and South Atlantic Fishery Management Councils 1982). Each uncertainty constitutes a serious recruitment problem, one because of difficulty in assuring continued larval influx without knowledge and control of parental stocks, and the other because of yield-per-recruit losses imposed by growth retardation and mortality of sublegal juveniles. This report reviews biological evidence and fishery regulations as related to stock origins and impacts to stocks. A brief summary of *P. argus* life history is provided to assist in explaining interactions between the resource and the fishery.

## Life History

*Panulirus argus* larvae inhabit oceanic waters where they pass through 11 stages (Lewis 1951; Baisre 1964), during a period estimated to be more than 6 mo (Sims and Ingle 1967), before they metamorphose to a transitional swimming stage termed a puerulus (Lyons 1980). *Panulirus argus* pueruli arrive along the south Florida coast during every month of the year (Little 1977; Little and Milano 1980; Menzies 1981) by swimming at night (Calinski and Lyons 1983) during dark lunar phases (Witham et al. 1968; Little and Milano 1980). Pueruli transit channels between the Florida Keys (Sweat 1968) to enter nursery areas in Florida Bay.

Young *P. argus* (approximately 6 mm carapace length (CL)) take up solitary residence in algal clumps (Marx and Herrnkind 1985a, 1985b). When they attain 15–16 mm CL, they enter holes and crevices in rocks, corals, and sponges (Davis 1978; Andree 1981, 1982; Marx and Herrnkind 1985a). At approximately 25–35 mm CL, lobsters abandon solitary residences to congregate in rocky dens (Davis 1978). Most of their remaining juvenile life is spent foraging and seeking shelter appropriate for their increasing size. Juveniles reside in nurseries for 15 mo (Calinski 1985) to 2 yr (Davis 1978). Biscayne Bay, Florida Bay, and oceanside shallows (≤3 m depths) of the Florida Keys are the principal south Florida nurseries supporting juveniles which will recruit to the legal fishery. Most lobsters in those areas are immature animals (Eldred et al. 1972; Warner et al. 1977; Davis 1978; Lyons et al. 1981) in residence or in transit toward adult habitat.

Older juveniles move from inshore nurseries and begin adult life after arrival at seaward reefs (Davis 1978; Lyons et al. 1981). Migratory routes from bays to reefs have been demonstrated through tagging studies (Little 1972; Warner et al. 1977; Davis and Dodrill 1980; J. M. Marx, unpubl. data) and by population size frequency progressions (Warner et al. 1977; Lyons et al. 1981). Average size in undisturbed adult popu-

lations is near 100 mm CL (Davis 1974), and resident adults exhibit only limited seasonal movements related to reproduction (Davis 1977). Reproductive activity, as indicated by females with spermatophores or eggs, is entirely an oceanside activity, and most mature lobsters occur near offshore reefs (Warner et al. 1977; Lyons et al. 1981; Gregory et al. 1982). Spawning occurs principally in deeper water seaward of the reefs, and larvae enter oceanic waters at or near those sites.

## Origins of the Stock

Hypotheses to explain origins of larvae providing recruitment to the south Florida fishery population include transport from the Caribbean via the Yucatan Channel and Florida Current, transport of larvae spawned in the Gulf of Mexico, and entrainment of larvae in a localized current, followed by transport back to the Florida coast. Attempts to verify these hypotheses have been frustrated by inability to distinguish between larvae of the three *Panulirus* species (*P. argus*, *P. guttatus*, and *P. laevicauda*) which occur in the region (Lyons and Little 1975; Richards and Potthoff 1981), by occurrence of *Panulirus* larvae in every developmental stage during every month of the year (Richards 1975), and by confusing results obtained from electrophoretic studies of protein enzyme systems and examinations of mitochondrial DNA among juvenile and adult *P. argus*. Most evidence related to each hypothesis was summarized by Lyons (1981), Menzies (1981), and Richards and Potthoff (1981) and is reviewed here only briefly.

### Caribbean Recruitment

Lewis (1951) speculated that most larvae from the Florida population are carried northward by the Florida Current, and late-stage larvae that occur off south Florida may have originated in the West Indies. Ingle et al. (1963), Sims and Ingle (1967), and Austin (1972) demonstrated *Panulirus* larvae to be abundant in waters exiting the Yucatan Strait and presented hydrographic evidence that those larvae could be transported to south Florida. However, it has not been demonstrated that larvae in that system are actually those which later arrive as pueruli along the south Florida coast. The fact that pueruli recruit to the Florida coast during every month of the year seems to support this hypothesis, because spawning occurs year-round in the Caribbean but only for approximately 6 mo in south Florida (Lyons et al. 1981; Gregory et al. 1982). Best evidence indicates that at least those recruits arriving in Florida when none are expected from Florida must originate elsewhere, probably in the Caribbean (Lyons 1981).

### Gulf of Mexico Recruitment

Some late-stage larvae in waters off south Florida may have originated in the Gulf of Mexico (Lewis 1951). Sims and Ingle (1967) and Austin (1972) found *Panulirus* larvae off the Florida west coast. Gulf of Mexico stocks of *Scyllarides nodifer*, a slipper lobster whose numbers of larval stages and larval period are similar to those of *P. argus*, undergo complete larval development within the Gulf of Mexico, and larvae from those stocks seemingly recruit to coastal waters of the Florida Keys and southeastern United States (Lyons 1981). Based upon demonstrated occurrence of large, reproductively active *P. argus* in the areas where parental stocks of *S. nodifer* occur, Lyons (1981) suggested that some larvae from those relatively unexploited *P. argus* could recruit to south Florida.

### Local Recruitment

Local eddies may be more important than major currents in transporting *P. argus* larvae (Smith 1948). Electrophoretic studies indicating genetic dissimilarity among juvenile and adult lobsters at several south Florida and Caribbean localities (Menzies et al. 1978) led Menzies and Kerrigan (1979) to propose a system of local recruitment loops wherein most *P. argus* larvae were returned to areas of origin. Johnson (1971) proposed a similar system for eastern Pacific *Panulirus* species. Entrainment of Florida larvae in a countercurrent/eddy system near the Florida Keys, transport into the Florida Loop Current, and subsequent transport back to the Keys was suggested to be the system maintaining local recruitment (Menzies and Kerrigan 1979, 1980). Other evidence obtained from restriction endonuclease analysis of mitochondrial DNA from juvenile and adult lobsters (Komm et al. 1982) also suggests dissimilar genetic composition of upper and lower Florida Keys lobsters (A. S. Michaels, Department of Biology, University of South Florida, Tampa, FL, unpublished report to FDNR), adding support to the hypothesis for local recruitment. However, Menzies (1981) found genetic similarity between Florida Keys, Mexico, and Trinidad lobsters and noted that those areas could provide recruits to Florida. Menzies acknowledged that year-round influx of pueruli to south Florida, together with seasonally restricted local spawning, challenged his local recruitment hypothesis. He conceded the level of foreign arrivals to be "in excess of 25%" but maintained that local selection might prevent the foreign contingent from becoming recruits to the Florida fishery.

In summary, the question of larval origins remains unresolved.

## Fishery Regulations

The *Fishery Conservation and Management Act* of 1976 divided management responsibility for the south Florida spiny lobster resource between the State of Florida and the United States federal government (Zuboy et al. 1980). Florida regulations pertinent to spiny lobster recruitment establish a closed harvest season, a minimum legal size, and an allowance for retention of sublegal-sized lobsters which fishermen transport aboard vessels for use as attractants in traps. Regulations in the federal spiny lobster fishery management plan (Gulf of Mexico and South Atlantic Fishery Management Councils 1982) do not differ from Florida statutes.

The State of Florida has maintained a closed harvest season since 1919. The closed season, now 1 April – 25 July, has been changed several times but always has occurred during some portion of the spring–summer spawning season.

Florida has maintained a minimum legal size since 1929. The only change in minimum size has been to a smaller size and seems to reflect the influence of the market (Davis 1980). Based upon reproductive information obtained in the fishery during the late 1940s, Dawson and Idyll (1951) recommended that the then-legal size of 1 lb (approximately 80 mm CL) be increased to 9 in. total length (83 mm CL), but the regulation was not changed. Reproductive information from a survey during the early 1960s prompted Robinson and Dimitriou (1963) to recommend a minimum legal size of $3\frac{1}{8}$ in. (79 mm) CL. At that time, fishery interests advocated a minimum size of $2\frac{3}{4}$ in. (70 mm) CL. The present minimum 3 in. (76 mm) CL was enacted in 1965, evidently as a compromise.

## Fishery Impacts on Yield-per-Recruit

Juvenile and adult spiny lobsters are gregarious, and fishermen have adopted the practice of confining sublegal-sized lobsters, i.e. "shorts," in traps as living attractants for legal-sized lobsters. Since 1976, fishermen have been allowed to possess 200 shorts aboard each vessel for use as attractants. Such lobsters are usually maintained in holding boxes until they are placed in traps and returned to the sea. When sufficient numbers of shorts are available, fishermen deploy three to five per trap, and as many as 1 million juveniles may be kept in traps during the height of the harvest season (Lyons and Kennedy 1981).

The number of traps deployed in the Florida spiny lobster fishery increased from 80 000 to 675 000 between 1963 and 1984, and annual catch per trap decreased from 45 lb. (20.5 kg) to 8 lb. (3.6 kg) during the same period. The increase in effort accelerated after the 1975 closure of the Bahamian Banks to American fishermen who, since the late 1960s, had landed increasingly greater numbers of "foreign" lobsters in Florida ports (Prochaska and Cato 1980; Simmons 1980). Those fishermen were displaced to south Florida, where they joined waves of Cuban immigrants entering the already crowded fishery (Labisky et al. 1980). Competition in the overcapitalized fishery has led to activities with serious ramifications to reproductive continuity and to recruitment into the legally harvestable stock. Additionally, the relatively great availability of sublegal lobsters and market demand for a small product have encouraged some fishermen to harvest the sublegal stock.

Lowering the minimum size prompted expansion of the fishery from oceanside areas into Florida Bay, where many previously undersized lobsters are now eligible for harvest. The portion of Florida Bay within Everglades National Park is closed to lobster harvest, and harvest is prohibited in most of Biscayne Bay, but approximately half of the south Florida fishery is conducted in Florida Bay waters where harvest is allowed (Gulf of Mexico and South Atlantic Fishery Management Councils 1982). The principal method of harvest in the south Florida fishery is with wood slat traps, although divers take at least 10% of the total catch (Davis and Dodrill 1980; Zuboy 1980; Lyons et al. 1981). High levels of harvest occur in shallow, bayside nursery areas where legal-sized lobsters seldom exceed 20% of trap catch (Lyons et al. 1981). Upon attaining sizes of approximately 50 mm CL, small lobsters begin to associate with larger juveniles in these areas (Davis 1981), and 50–75 mm CL lobsters are encountered most frequently by divers and in traps (Lyons et al. 1981). Harvest of those lobsters and their use as attractants each contributes to mortality. Additional detriments to recruitment accrue from fishery-induced growth retardation and subsequently reduced reproductive contributions.

### Reproduction

Impact of the present minimum legal size on larval production has been considerable. Results of studies at Venezuela, Antigua and Barbuda, Puerto Rico, Jamaica, the Bahamas, south Florida, and Bermuda indicate that most *P. argus* in those populations do not spawn until they attain sizes greater than the Florida minimum legal size of 76 mm CL; sizes at which most lobsters attain capability to spawn have been reported to be 80–90 mm CL (Peacock 1974), 86–95 mm CL (Davis 1974, 1975), 96–100 mm CL (Kanciruk and Herrnkind 1976), and 90–95 mm CL (Sutcliffe 1952, 1953, 1957; Feliciano 1958; Munro 1974; Aiken 1977; Lyons et al. 1981). Weber (1968) studied development of "ovigerous setae" (setae on pleopods of adult lobsters, used to maintain the egg mass beneath the abdomen) and estimated that 50% maturity among female *P. argus* at Belize occurs at approximately 88 mm CL. Using the same technique, Gregory and Labisky (1981) reported that most south Florida *P. argus* attain fully developed ovigerous setae in the 85–90 mm CL size class. However, histological examination of ovaries indicates that most south Florida *P. argus* become reproductively active at sizes of 90–95 mm CL (S. F. Barber, unpubl. data).

Fecundity is proportional to spiny lobster size (Mota Alves and Bezerra 1968), and the amount of larvae produced by any population is influenced by the numbers and sizes of lobsters in that population. In Florida, where most lobsters are harvested at or slightly above minimum legal size, very few lobsters survive to sizes ≥90 mm CL (Lyons et al. 1981). As a result, much of the spawning stock is composed of the relatively few, less fecund lobsters that mature at small sizes. During 1975–76, 64% of all eggs in the lower Florida Keys were produced by lobsters <85 mm CL (Gregory et al. 1982). Lobsters ≤85 mm CL produced 59.4% of all eggs in the middle and upper Keys during 1978, and 78.5% of all spawn was produced by lobsters ≤90 mm CL; only 10.6% of all spawning females were >90 mm CL (Lyons et al. 1981). An Index of Reproductive Potential (Kanciruk and Herrnkind 1976) indicates that egg production by lobsters in the middle and upper Keys during 1978 was reduced 88% from that expectable from an unexploited population (Lyons et al. 1981). Undiminished recruitment, in the presence of such reproductive decline, supports the hypothesis that most larvae recruited to Florida originate in the Caribbean area (Lyons et al. 1981; Waugh 1981).

No aforementioned study considered additional annual egg production due to repetitive spawning. *Panulirus argus* at Bermuda spawn twice during a season (Creaser 1950); a second spawn may contain fewer than half the number of eggs produced by a first spawn, but still constitutes an important contribution to total larval production. In south Florida, spiny lobsters approaching maturity molt during spring and produce only a single spawn during summer whereas larger, previously mature lobsters spawn during spring and again during summer (Lipcius 1986). Early in the history of the Florida fishery, Crawford and De Smidt (1922) noted that largest lobsters spawned earliest during the season. This was confirmed by Davis (1975), who reported a 55% incidence of early spring spawning among the partially protected population of large females ($\bar{x}$ = 97 mm CL) at Ft. Jefferson National Monument, Dry Tortugas; during April 1973–75, 73% of 826 lobsters 96–135 mm CL were spawning whereas only 25% of 244 lobsters 76–85 mm CL and 60% of 344 lobsters 86–95 mm CL carried eggs. The spring spawn by highly fecund large lobsters virtually has been eliminated in the south Florida fishery population due to removal of lobsters before they attain such sizes.

### Growth Retardation

Growth rates of spiny lobsters involve both the amount of size increase (growth increment) and the interval between molts (intermolt period). When antennae or legs are lost or other injuries are sustained by spiny lobsters, energy normally

directed toward growth may be redirected toward regeneration and repair (Chittleborough 1975; Davis 1981; Brown and Caputi 1985). Average growth increment decreased 10% and intermolt period increased 50% among injured juvenile *P. argus* in Biscayne Bay (Davis 1981). Annual growth rates of injured lobsters were 40% less than those of uninjured lobsters, and 40.3% of the population sustained some injury; most injuries were attributed to recreational divers. Davis (1981) predicted that a 50 mm CL lobster that sustained an injury would require an additional 33 wk to attain legal size. When natural mortality was considered, about 22% of the injured lobsters would be lost to fishery recruitment because of their injuries. Waugh (1981) found similar injury-induced growth retardation (28–51%, males; 13–25%, females) among *P. argus* at Grand Bahama Island; retardation rates varied by lobster size, gender, and habitat. However, injury-related growth retardation in the Florida Keys fishery population may not be so severe. Davis and Dodrill (1980) found growth rates of injured lobsters in Everglades National Park (Florida Bay) to be only 6.3% less than those of uninjured lobsters; average incidence of injury among the population was only 13%. They concluded that better growth conditions and minimal disturbance reduced effects of injuries there. Similar rates of injury (10.4%) and decreased growth (4.3%) of injured juvenile lobsters (50–75 mm CL) were observed in the commercially fished middle and upper Florida Keys population during 1978–79 (Lyons et al. 1981; J. H. Hunt, unpubl. data). Using the rationale of Davis (1981), entry of those lobsters into the legal fishery would be delayed a maximum of 4–5 wk beyond that of uninjured lobsters, and increased loss due to natural mortality would be approximately 3%.

Confinement in fishery traps may be more important than injury as a contributor to growth retardation and recruitment loss. Marshall (1948) reported nine instances in which *P. argus* confined in "live cars" exhibited little or no increase in length or weight after molting; weight loss was documented in six of the cases. Lyons and Kennedy (1981) documented weight loss among nonmolting *P. argus* confined at densities of three or five per trap for periods of 1–8 wk; weight losses increased over time and were greater at the higher density. In an experiment involving tagged lobsters released or used as attractants in traps, confined lobsters averaged 28% smaller growth increments, and intermolt periods were more than twice longer (35.7 vs. 15.4 wk) than those of unconfined lobsters (F. S. Kennedy et al., unpubl. data). The intermolt period of lobsters confined as attractants was approximately the same as the entire 36-wk harvest season, and growth, when it did occur, was considerably less than normal.

Growth retardation increases the probability that sublegal-sized lobsters will not enter the legal fishery but, instead, will be removed by natural mortality (Davis 1981; Brown and Caputi 1985), illegal harvest, or mortality related to use as attractants before attaining legal size. Furthermore, because maturity is more a function of age than of size (Chittleborough 1974), whereas fecundity is directly related to size, sizes of mature lobsters will be reduced in areas of intense fishing activity (Davis 1981), and fecundity will be reduced proportional to reduced sizes (Morgan 1972; Brown and Caputi 1985). Numbers of *P. argus* spawning at increasingly smaller sizes (Warner et al. 1977; Lyons et al. 1981) indicate that this is occurring in south Florida, further reducing fecundity of that population (Davis 1981).

### Illegal Harvest

Fishermen estimate the magnitude of the illegal short fishery to be 20–50% that of the legal fishery (Gulf of Mexico and South Atlantic Fishery Management Councils 1982). The number of lobsters lost to the fishery due to illegal harvest is unknown, but arrests for possession of thousands of pounds of sublegal-sized lobsters demonstrate the existence of the practice. Although illegal landings generate revenue for fishermen, economic losses in terms of yield-per-recruit may be considerable. Average annual Florida landings during 1975–83 were 6.12 million lb (2.78 million kg) (J. E. Powers and S. P. Bannerot, National Marine Fisheries Service Summary to Gulf of Mexico Fishery Management Council, May 1984). If illegal harvest was 20% of that amount, an average 1.224 million lb (555 000 kg) of sublegal lobsters also were landed annually. Most sublegal lobsters in traps range in size from 65 to 75 mm CL (median = 70 mm CL). Using the conversion $W = 0.00422CL^{2.64091}$ (Lyons et al. 1981), average weight of a 70 mm CL lobster is 315 g, so the 1.224 million lb harvested at sublegal size may be presumed to have comprised approximately 1 764 114 lobsters. Those 70 mm CL lobsters would grow 6 mm CL and attain legal size in at most 15 wk. Assuming annual natural mortality of 34.8% (Olsen and Koblic 1975; Davis 1981), 10% of the lobsters should die during a 15-wk period. The remaining 90% of now-legal lobsters should weigh 1 368 600 lb (620 000 kg), a net gain of 144 600 lb (65 727 kg). At average dockside prices (US$2.50/lb), those now-legal lobsters would be worth an additional $361 500 to the fishery. If magnitude of the short fishery is 50% rather than 20%, anual losses in yield-per-recruit would be worth $903 750.

### Mortality of Attractants

Many lobsters confined as attractants in traps die of exposure-induced trauma, starvation, or predation. These problems first became evident when Yang and Obert (1978) noted that total mortality rates of sublegal and legal lobsters in the lower Florida Keys during the mid-1970s were almost identical. They concluded that numbers of sublegal and legal lobsters removed from the population were similar and concluded that juvenile lobsters had a very high mortality rate. Based upon injury rates of legal and sublegal lobsters, Lyons et al. (1981) concluded that most sublegal lobsters injured in the middle and upper Keys fishery during 1978–79 did not return to the wild population.

During 1978–79, significant short-term mortality was discerned among lobsters confined in traps (Lyons and Kennedy 1981). This prompted an experiment in which lobsters were exposed in shaded boxes aboard vessels for various periods and then placed in sealed traps at Florida Bay and Atlantic reef sites. In Florida Bay, 21% of all lobsters exposed 0.5, 1, 2, or 4 h died in traps within 4 wk; mortality rates (0 h (controls) = 2.2%, 0.5 h = 11.8%, 1 h = 24.1%, 2 h = 22.1%, 4 h = 25.6%) were related to exposure periods. Mortality rates of lobsters exposed 1, 2, or 4 h were not significantly different, but average mortality of those lobsters was approximately twice that of lobsters exposed 0.5 h. Average mortality rates at the reef site after 4 wk (0 h = 13.6%, 0.5 h = 26.0%, 1 h = 45.3%, 2 h = 27.1%, 4 h = 31.8%) confirmed the relationship between exposure and death. Average mortality of lobsters exposed 0.5–4 h at both sites was 26.3% after 4 wk. Mortality

rate was not related to air or water temperature (Lyons and Kennedy 1981), and dampening exposed lobsters did not improve survival (Hunt et al. 1986).

Approximately 42% of all mortality occurred within 1 wk following test initiations, indicating exposure to be a principal cause of lobster deaths. When mortality rates of controls were subtracted from those of exposed lobsters, resultant values (18.6%, Florida Bay; 18.3%, reef) were nearly identical and probably represent actual rates of mortality ascribable to exposure (Hunt et al. 1986). The greater level of mortality that occurred among all lobsters, including controls, during wk 1−3 and the marked increase that occurred during wk 4 indicated that factors other than exposure caused additional mortality at the reef site. Lesser availability of food organisms (e.g. snails, crabs) entering traps probably accelerated starvation and increased mortality of reef lobsters during wk 4; other causes of death remain unknown (Hunt et al. 1986).

No data exist to indicate the impact of predators on lobsters confined as attractants in traps. Although juvenile lobsters in their natural environment may be required to escape from predators, escape may be more difficult or impossible for lobsters confined as attractants. In one instance observed by divers, a triggerfish entered a trap containing four attractants and killed and ate each lobster in turn (J. H. Hunt, pers. comm.). Octopus also kill lobsters in traps (Lyons and Kennedy 1981). During periods when a million sublegal lobsters are confined in traps (Lyons and Kennedy 1981), impact of predators on those potential fishery recruits is probably considerable. If so, that impact is additive to those caused by exposure and starvation.

Attractant mortality is difficult to discern in fishery situations. Traps usually are pulled on weekly schedules whereas carcasses of lobsters that die in traps may be so reduced by scavengers that the pieces wash through trap slats within 24 h (Hunt et al. 1986). The subsequent absence of dead lobsters when traps are pulled has encouraged fishermen to believe that missing lobsters simply escape. However, spiny lobsters have difficulty exiting traps (Miller and Sutherland 1978), and escape rates average only 1−3% nightly in the Florida fishery (Yang and Obert 1978; Davis and Dodrill 1980; Lyons and Kennedy 1981; J. H. Hunt, unpubl. data), so most lobsters missing from fishermen's traps may be presumed to have fallen victim to exposure, starvation, or predation.

A study of baiting effectiveness under fishery conditions provided additional insight into the fate of attractants. Using tag and recovery techniques, F. S. Kennedy et al. (unpubl. data) compared recovery rates of lobsters captured and immediately released, lobsters used as attractants and then deliberately released, and lobsters that disappeared from traps while being used as attractants. Recovery rates of tagged lobsters among the first two groups were virtually identical (18.0 vs. 18.8%), indicating little difference in probability of return among lobsters deliberately released, but the recovery rate of lobsters that disappeared was significantly lower (10.6%). From that difference, Kennedy et al. calculated the number of missing lobsters that probably died, added to that the number of known deaths (i.e. carcasses observed in traps), and concluded that total mortality of lobsters used as attractants in that experiment was 47%.

The Western Australia rock lobster fishery, based upon *Panulirus cygnus*, is arguably the largest and most effectively managed of spiny lobster fisheries. Even though gaps to facilitate juvenile escape are required in traps of that fishery, an estimated 16−20 million sublegal lobsters are brought aboard vessels and exposed for various periods before being released. Results of tag and recapture experiments revealed significantly greater injury and mortality rates among sublegal rock lobsters exposed before being returned to the sea; exposed lobsters also were much more susceptible to predation by octopus and fish (Brown and Caputi 1983). Exposure and injury each reduced subsequent growth increments significantly (Brown and Caputi 1985). Fishery-induced mortality was estimated to reduce rates of recapture 14.6% and to cost the fishery A$8 million in annual landings (Brown and Caputi 1983, 1985).

The Western Australia Department of Fisheries and Wildlife suggested that drying of gills during exposure caused respiratory problems that led to mortality of *P. cygnus*; they recommended that lobsters be returned to the sea as soon as possible or, if that was impractical, that fishermen use sprinkler systems aboard vessels to reduce effects of exposure (Anonymous 1980, 1981). However, dampening exposed lobsters may be of little value; *P. argus* dampened at 0.5-h intervals died at rates similar to those of lobsters left unattended (Hunt et al. 1986). Although moist air improved survival of exposed northern lobsters, *Homarus americanus*, dampening by continuous seawater spraying failed to improve survival rates (McLeese 1965). McLeese proposed that there is an inverse relationship between metabolic rate and survival time among exposed lobsters. Supportive evidence for this relationship has been provided by G. K. Vermeer (FDNR, unpubl. data), who examined several aspects of *P. argus* hemolymph chemistry to identify physiological effects that might contribute to exposure-induced mortality. Dramatic metabolic changes correlated with length of exposure were observed in hemolymph pH and lactic acid and ammonia levels among *P. argus* exposed 0.5, 1, or 2 h in open shade. Although hemolymph levels returned to normal within 24 h, lobsters that had been exposed displayed severely impaired escape responses. Vermeer concluded that nervous system damage induced by hypoxia, acidosis, and perhaps osmotic imbalances was the likely cause of mortality.

## Conclusions and Recommendations

The present minimum legal size has resulted in extreme reduction of reproductive contributions by the south Florida fishery stock. Those contributions can be increased by raising the minimum size, probably to 85−90 mm CL. The fishery management plan for *P. argus* in Puerto Rico and the U.S. Virgin Islands has established a 3.5 in. (89 mm) CL minimum size in that fishery (Caribbean Fishery Management Council 1981). An increase of minimum size from 76 to 85 mm CL for Florida *P. argus*, to be effected in small annual increments to mitigate economic impacts (Gregory et al. 1982), is an appropriate first step toward recovery of the spawning stock.

With regard to protection during the spawning season, extension of the present closure (1 April − 25 July) through August would protect the 10% level of spawning which continues then (Gregory 1979). However, 77−85% of all spawning occurs during the present closed season (Lyons et al. 1981; Gregory et al. 1982). Any spawning gains that will accrue from larger lobsters in response to a minimum size increase probably will occur early in the closed season, so it may not be necessary to extend closure through August if minimum size is increased.

In addition to protecting reproductively active lobsters, the closed season allows replenishment by growth such that legal-sized stocks recover to a much higher level by the time the

season reopens, thereby facilitating more efficient harvest (Lyons 1981). For that reason alone, the closed season is an effective management strategy, and extending that closure through August would allow even greater stock recovery.

Uncertainty regarding origins of larvae calls to question the necessity to protect any of Florida's spawn. If principal recruitment sources are local, local spawn must be protected. However, at least a significant portion of Florida's recruitment probably originates in the Caribbean region, and it is not known that any larvae spawned in the Florida fishery area actually return there. Nevertheless, this does not negate the necessity to protect spawning stock. The western Atlantic populations of *P. argus* constitute a Pan-Caribbean resource. As harvest increases in each national fishery, it will become increasingly important that larval production remains sufficient to provide recruitment to whatever fishable population it has previously supported (Jones 1975). Florida would appear to be especially vulnerable as regards dependence upon external recruitment (Lyons and Little 1975). In this case, it would seem prudent for management to lead by example.

The south Florida spiny lobster fishery depends upon sublegal lobsters to bait traps. Sublegal lobsters attract other lobsters more effectively than do other baits. Live lobsters do not attract stone crabs (which compete with lobsters in traps) as do other baits, and, by feeding on sessile biota, attractants clean the insides of traps, which fishermen believe improves trap effectiveness. As operational costs continue to rise, fishermen perceive the cost of attractants to be free. Consequently, fishermen have been reluctant to accept results of research that indicate the deleterious effects of their baiting technique.

A statistical model by Austin et al. (1980) indicated that legal landings in the south Florida fishery should have been 103% greater than those actually reported in commercial landings; the deficit of "missing" lobsters was attributed to unreported commercial landings, recreational landings, and illegal harvest. However, it since has become clear that fishery-induced growth retardation and mortality of sublegal stock contribute greatly to yield-per-recruit losses.

Evidence of injury-induced growth retardation is mixed. Severe injury-related growth reductions at Biscayne Bay (40%; Davis 1981) and Grand Bahama Island (13–51%; Waugh 1981) seemingly are contradicted by evidence that growth of Florida Bay lobsters is affected only slightly (4.3–6.3%) by injuries (Davis and Dodrill 1980; J. H. Hunt, unpubl. data). The discrepancy may be explained by exceptionally favorable growth conditions in Florida Bay (Davis and Dodrill 1980). However, lobsters confined as attractants in traps are denied the benefits of favorable surroundings. Confinement leads to weight loss among nonmolting lobsters (Lyons and Kennedy 1981) and results in smaller growth increments and extended intermolt periods among lobsters that molt (Marshall 1948; F. S. Kennedy et al., unpubl. data). The only food sources available to confined lobsters are organisms which crawl into traps, sessile biota which settle on insides of traps, or other lobsters which molt or die in traps. Starvation rates vary by area in response to availability of food organisms which enter traps (Hunt et al. 1986). Lobsters that clean the insides of traps may be utilizing the only food source available to them. Although starvation-related growth reductions have not been studied thoroughly, and thus are not quantifiable, resultant losses in terms of yield-per-recruit must be considerable.

Evidence of mortality caused by exposure and confinement is much stronger. On the average, more than 26% of all lobsters exposed 0.5–4 h and then placed in traps will die within 4 wk (Hunt et al. 1986), and 47% may die if left in traps indefinitely (F. S. Kennedy et al., unpubl. data). If the overall mortality rate of lobsters used as attractants is 40%, a seemingly reasonable estimate, yield-per-recruit losses will be in the range of 20–50% (J. E. Powers and S. P. Bannerot, U.S. National Marine Fisheries Service summary to Gulf of Mexico Fishery Management Council, May 1984). Powers and Bannerot identified mortality of attractants as the single most influencial factor depressing yield in the Florida fishery.

Installation of escape gaps in traps may be the single most effective management strategy to reduce fishery-induced yield-per-recruit losses (Brown and Caputi 1985). Gaps designed to allow most sublegal lobsters to escape while retaining most legal-sized lobsters effectively will reduce access by fishermen to the sublegal stock (Waugh 1981). If access to sublegal stock is reduced significantly, availability of shorts for use as attractants will decline and illegal harvest of undersized lobsters will be rendered more difficult. Results of tests in the south Florida fishery area indicate that height of an appropriate gap should be in the range of 2–2$\frac{1}{8}$ in. (51–54 mm) (J. H. Hunt, unpubl. data).

Much fishing effort is expended now in areas that serve principally as lobster nurseries. Greatest yield-per-recruit losses probably occur in those nurseries; sublegal lobsters are abundant there, but legal catches are quite low and occur only during a few months of the year (Lyons et al. 1981). If minimum legal size is increased or escape gaps are required, harvest in those areas may become even less feasible in terms of fishery costs and effort, and fishermen may be compelled to relocate to more profitable areas. If the fishery does not relocate, designation of nurseries as sanctuaries may be required.

The basic problem in the south Florida fishery is that the industry continues to direct more capital and effort toward a finite stock. Increased competition undoubtedly contributes to attitudes among some fishermen that condone illegal harvest and advocate other practices conducive to stock reductions through growth retardation and mortality. Harvest effort must be reduced, if for no other reason than to reduce the cost of doing business. If fishery expenses are reduced, profits will rise. However, higher profits inevitably will attract more entrants into the fishery, so some form of limited entry will be required. Austin (1981) reviewed problems and options for limiting entry in the Florida spiny lobster fishery.

Success of any management strategy will depend upon the ability to enforce regulations and, particularly, upon the willingness of fishery participants to comply with those regulations. Agencies charged with enforcement of fishery regulations in south Florida are understaffed and underfunded; that situation must be improved. Ultimately, however, educational programs must be initiated to convey to fishermen the implications of present harvest practices and to engender a positive attitude toward long-term resource productivity.

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sized spiny lobsters, with notes on effects of confinement"; J. M. Marx, "Movement dynamics of spiny lobsters in the Florida Keys"; and G. K. Vermeer, "Effects of air exposure on desiccation rate, hemolymph chemistry and escape behavior of the spiny lobster." Dr. R. N. Lipcius, Smithsonian Environmental Research Center, Edgewater, Maryland, also provided access to his manuscript in press. All are gratefully thanked. Funding for the various FDNR studies was provided in part by the U.S. Department of Commerce, National Marine Fisheries Service, through PL 88-309, Project No. 2-341-R.

## References

AIKEN, K. A. 1977. Jamaica spiny lobster investigations, p. 11–12. *In* Symposium on progress in marine research in the Caribbean and adjacent regions. FAO Fish. Rep. 200, Caracas.

ANDREE, S. W. 1981. Locomotory activity patterns and food items of benthic postlarval spiny lobster, *Panulirus argus*. M.Sc. Thesis, Florida State University, Tallahassee, FL. 50 p.

1982. Foraging activity patterns and food items of post-puerulus spiny lobsters, *Panulirus argus*, p. 6. *In* W. G. Lyons [ed.] Proceedings of a workshop on Florida spiny lobster research and management, 13–14 August 1981. Florida Department of Natural Resources, St. Petersburg, FL.

ANONYMOUS. 1980. The fate of undersized rock lobsters returned to the sea. W. Aust. Dep. Fish. Wildl. Fish. Ind. News Serv. 13: 10–12.

1981. Handling techniques costing W.A. rock lobster fishermen about $6.2 million a year. Western Australia Department of Fisheries and Wildlife, Perth. 4 p.

AUSTIN, C. B. 1981. Difficulties of limiting entry in the over-capitalized south Florida spiny lobster fishery. Proc. Gulf Caribb. Fish Inst. 33: 184–200.

AUSTIN, C. B., G. T. WAUGH, AND S. K. CHAN. 1980. Estimation of unrecorded spiny lobster, *Panulirus argus*, catch from recorded landings, p. 61–98. *In* C. B. Austin. Bio-economic and legal analysis for alternative policies for limited entry into the Florida spiny lobster fishery. Final report, Ford Foundation Program in Policy Analysis for State Environmental Management. University of Miami, Miami, FL.

AUSTIN, H. M. 1972. Notes on distribution of phyllosoma of the spiny lobster *Panulirus* ssp. in the Gulf of Mexico. Proc. Natl. Shellfish Assoc. 62: 26–30.

BAISRE, J. A. 1964. Sobre los estudios larvales comun, *Panulirus argus*. Contrib. Inst. Nat. Pesca Cuba No. 19: 37 p.

BROWN, R. S., AND N. CAPUTI. 1983. Factors affecting the recapture of undersize western rock lobster *Panulirus cygnus* George returned by fishermen to the sea. Fish. Res. 2: 103–128.

1985. Factors affecting the growth of undersize western rock lobster, *Panulirus cygnus* George, returned by fishermen to the sea. Fish. Bull. (U.S.) 83: 567–574.

CALINSKI, M. D. 1985. Settlement, growth and survival of puerulus to juvenile stage spiny lobsters in artificial nursery habitats and potential application of such habitats to Florida's fishery, p. 1–3. *In* W. F. Herrnkind [ed.] Proceedings of a workshop on Florida spiny lobster research and management, 24 August 1984. Florida State University, Tallahassee, FL.

CALINSKI, M. D., AND W. G. LYONS. 1983. Swimming behavior of the puerulus of the spiny lobster *Panulirus argus* (Latreille, 1804) (Crustacea: Palinuridae). J. Crustacean Biol. 3: 329–335.

CARIBBEAN FISHERY MANAGEMENT COUNCIL. 1981. Environmental impact statement/fishery management plan and regulatory impact review for the spiny lobster fishery of Puerto Rico and the U.S. Virgin Islands. Hato Rey, Puerto Rico.

CHITTLEBOROUGH, R. G. 1974. Western rock lobster reared to maturity. Aust. J. Mar. Freshwater Res. 25: 221–225.

1975. Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne Edwards). Aust. J. Mar. Freshwater Res. 26: 177–196.

CRAWFORD, D. R., AND W. J. J. DE SMIDT. 1922. The spiny lobster, *Panulirus argus*, of southern Florida, its natural history and utilization. Bull. Bur Fish. (U.S.) 38: 281–310.

CREASER, E. P. 1950. Repetition of egg laying and number of eggs of the Bermuda spiny lobster. Proc. Gulf Caribb. Fish. Inst. 2: 30–31.

DAVIS, G. E. 1974. Notes on status of spiny lobsters, *Panulirus argus*, at Dry Tortugas, FL, 1974, p. 22–32. *In* W. Seaman, Jr. and D. Y. Aska [ed.] Conference proceedings: research and information needs of the Florida spiny lobster fishery. State Univ. Syst. Fla. Sea Grant Rep. SUSF-SG-74-201, Gainesville, FL.

1975. Minimum size of mature spiny lobster, *Panulirus argus*, at Dry Tortugas, Florida. Trans. Am. Fish. Soc. 104: 675–676.

1977. Effects of recreational harvest on a spiny lobster, *Panulirus argus*, population. Bull. Mar. Sci. 27: 233–236.

1978. Management recommendations for juvenile spiny lobsters, *Panulirus argus*, in Biscayne National Monument, Florida. U.S. Natl. Park Serv. S. Fla. Res. Center Rep. M-530: 32 p.

1980. Juvenile spiny lobster management; or, how to make the most of what you get. Fisheries 5(4): 57–59.

1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fish. Bull. (U.S.) 78: 979–984.

DAVIS, G. E., AND J. W. DODRILL. 1980. Marine parks and sanctuaries for spiny lobster fisheries management. Proc. Gulf Caribb. Fish. Inst. 32: 194–207.

DAWSON, C. E., AND C. P. IDYLL. 1951. Investigations on the Florida spiny lobster, *Panulirus argus* (Latreille). Fla. Board Conserv. Tech. Ser. 2: 39 p.

ELDRED, B., C. R. FUTCH, AND R. M. INGLE. 1972. Studies of juvenile spiny lobsters, *Panulirus argus*, in Biscayne Bay, Florida. Fla. Dep. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 35: 15 p.

FELICIANO, C. 1958. The lobster fishery of Puerto Rico. Proc. Gulf Caribb. Fish. Inst. 10: 147–156.

GREGORY, D. R. JR. 1979. Reproductive dynamics of the spiny lobster, *Panulirus argus* (Latreille), in south Florida. Sea Grant '70s, 9(12): 14–15.

GREGORY, D. R. JR., AND R. F. LABISKY. 1981. Ovigerous setae as an indicator of reproductive maturity in the spiny lobster, *Panulirus argus* (Latreille). Northeast Gulf Sci. 4: 109–113.

GREGORY, D. R. JR., R. F. LABISKY, AND C. L. COMBS. 1982. Reproductive dynamics of the spiny lobster *Panulirus argus* in south Florida. Trans. Am. Fish. Soc. 111: 575–584.

GULF OF MEXICO AND SOUTH ATLANTIC FISHERY MANAGEMENT COUNCILS. 1982. Fishery management plan, environmental impact statement and regulatory impact review for spiny lobster in the Gulf of Mexico and south Atlantic. Tampa, FL.

HUNT, J. H., W. G. LYONS, AND F. S. KENNEDY, JR. 1986. Effects of exposure and confinement on spiny lobsters, *Panulirus argus*, used as attractants in the Florida trap fishery. Fish. Bull. (U.S.) 84: 69–76.

INGLE, R. M., B. ELDRED, H. W. SIMS, JR., AND E. ELDRED. 1963. On the possible Caribbean origin of Florida's spiny lobster populations. Fla. State Board Conserv. Mar. Lab. Tech. Ser. 40: 12 p.

JOHNSON, M. W. 1971. The palinurid and scyllarid lobster larvae of the tropical eastern Pacific and their distribution as related to the prevailing hydrography. Bull. Scripps Inst. Oceanogr. 19: 1–36.

JONES, A. C. 1975. Recruitment, p. 5. *In* W. Seaman and A. C. Jones [ed.] Review of spiny lobster research, including results and recommendations of a coloquium held October 1 and 2 in Miami, FL. Florida Sea Grant, Gainesville, FL.

KANCIRUK, P., AND W. F. HERRNKIND. 1976. Autumnal reproduction in the spiny lobster, *Panulirus argus*, at Bimini, Bahamas. Bull. Mar. Sci. 26: 417–432.

KOMM, B., A. MICHAELS, J. TSOKOS, AND J. LINTON. 1982. Isolation and characterization of the mitochondrial DNA from the Florida spiny lobster, *Panulirus argus*. Comp. Biochem. Physiol. 73B: 923–929.

LABISKY, R. F., D. R. GREGORY, JR., AND J. A. CONTI. 1980. Florida's spiny lobster fishery: an historical perspective. Fisheries 5(4): 28–37.

LEWIS, J. B. 1951. The phyllosoma larvae of the spiny lobster, *Panulirus argus*. Bull. Mar. Sci. Gulf Caribb. 1: 89–103.

LIPCIUS, R. M. 1986. Size-dependent reproduction and molting in spiny lobsters and other long-lived decapods. *In* A. Wenner [ed.] Crustacean issues. Vol. 2. Growth. Balkema Press, Rotterdam. (In press)

LITTLE, E. J. JR. 1972. Tagging of spiny lobsters (*Panulirus argus*) in the Florida Keys, 1967–69. Fla. Dep. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 31: 23 p.

1977. Observations on recruitment of postlarval spiny lobsters, *Panulirus argus*, to the south Florida coast. Fla. Mar. Res. Publ. 29: 35 p.

LITTLE, E. J. JR., AND G. R. MILANO. 1980. Techniques to monitor recruitment of postlarval spiny lobsters, *Panulirus argus*, to the Florida Keys. Fla. Mar. Res. Publ. 37: 16 p.

LYONS, W. G. 1980. The postlarval stage of scyllaridean lobsters. Fisheries 5(4): 47–49.

1981. Possible sources of Florida's spiny lobster population. Proc. Gulf Caribb. Fish. Inst. 33: 253–266.

LYONS, W. G., D. G. BARBER, S. M. FOSTER, F. S. KENNEDY, JR., AND G. R. MILANO. 1981. The spiny lobster, *Panulirus argus*, in the middle and upper Florida Keys: population structure, seasonal dynamics and reproduction. Fla. Mar. Res. Publ. 38: 38 p.

LYONS, W. G., AND F. S. KENNEDY, JR. 1981. Effects of harvest techniques

on sublegal spiny lobsters and on subsequent fishery yield. Proc. Gulf Caribb. Fish. Inst. 33: 290–300.

LYONS, W. G., AND E. J. LITTLE, JR. 1975. Problems and potentials of research on phyllosoma larvae of Florida spiny lobsters, p. 7–8. *In* W. Seaman and A. C. Jones [ed.] Review of spiny lobster research, including results and recommendations of a colloquium held October 1 and 2 in Miami, FL. Florida Sea Grant, Gainesville, FL.

MARSHALL, N. 1948. The molting without growth of spiny lobsters, *Panulirus argus*, kept in a live car. Trans. Am. Fish. Soc. 75: 267–269.

MARX, J. M., AND W. F. HERRNKIND. 1985a. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters. *Panulirus argus*. Bull. Mar. Sci. 36: 423–431.

1985b. Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. J. Crustacean Biol. 5: 650–657.

MCLEESE, D. W. 1965. Survival of lobsters, *Homarus americanus*, out of water. J. Fish. Res. Board Can. 22: 385–394.

MENZIES, R. A. 1981. Biochemical population genetics and the spiny lobster larval recruitment problem: an update. Proc. Gulf Caribb. Fish. Inst. 33: 230–243.

MENZIES, R. A., AND J. M. KERRIGAN. 1979. Implications of spiny lobster recruitment patterns of the Caribbean — a biochemical approach. Proc. Gulf Caribb. Fish Inst. 31: 164–178.

1980. The larval recruitment problem of the spiny lobster. Fisheries 5(4): 42–46.

MENZIES, R. A., J. M. KERRIGAN, AND P. KANCIRUK. 1978. Biochemical systematics and problems of larval recruitment in the spiny lobster, *Panulirus argus*, p. 22–30. *In* R. E. Warner [ed.] Spiny lobster research review; proceedings of a conference held December 16, 1976 in Key West, Florida. Fla. Sea Grant Tech. Pap. 4.

MILLER, G. C., AND D. L. SUTHERLAND. 1978. Behavior of the Florida spiny lobster, *Panulirus argus*, to baited Florida and prototype traps, p. 15–20. *In* R. E. Warner [ed.] Spiny lobster research review: proceedings of a conference held December 16, 1976 in Key West, Florida. Fla. Sea Grant Tech. Pap. 4.

MORGAN, G. R. 1972. Fecundity in the western rock lobster, *Panulirus longipes cygnus* (George) (Crustacea: Decapoda: Palinuridae). Aust. J. Mar. Freshwater Res. 23: 133–141.

MOTA ALVES, M. I., AND R. C. F. BEZERRA. 1968. Sobre o numero de ovos da lagosta *Panulirus argus* (Latr.). Arq. Estac. Biol. Mar. Univ. Fed. Ceara 8: 33–35.

MUNRO, J. L. 1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Sci. Rep. ODA/UWI Fish. Ecol. Res. Proj., 1969–73. Pt. V.1. The biology, ecology and bionomics of Caribbean reef fishes: VI. Crustaceans (spiny lobsters and crabs). Univ. W. Indies Zool. Dep. Res. Rep. 3, Kingston, Jamaica. 57 p.

OLSEN, D. A., AND I. G. KOBLIC. 1975. Population dynamics, ecology and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S.V.I.: II. Growth and mortality, p. 17–21. *In* S. A. Earle and R. J. Lavenberg [ed.] Results of the Tektite program: coral reef invertebrates and plants. Nat. Hist. Mus. Los Ang. Cty. Sci. Bull. 20.

PEACOCK, N. A. 1974. A study of the spiny lobster fishery of Antigua and Barbuda. Proc. Gulf Caribb. Fish. Inst. 26: 117–130.

PROCHASKA, F. J., AND J. C. CATO. 1980. Economic considerations in the management of the Florida spiny lobster fishery. Fisheries 5(4): 53–56.

RICHARDS, W. J. 1975. Research on the young stage of spiny lobsters: review and outlook, p. 9. *In* W. Seaman and A. C. Jones [ed.] Review of spiny lobster research, including results and recommendations of a colloquium held October 1 and 2 in Miami, FL. Florida Sea Grant, Gainesville, FL.

RICHARDS, W. J., AND T. POTTHOFF. !981. Distribution and seasonal occurrence of larval pelagic stages of spiny lobsters (Palinuridae, *Panulirus*) in the western tropical Atlantic. Proc. Gulf Caribb. Fish. Inst. 33: 244–252.

ROBINSON, R. K., AND D. E. DIMITRIOU. 1963. The status of the Florida spiny lobster fishery, 1962–1963. Fla. State Board Conserv. Mar. Lab. Tech. Ser. 42: 27 p.

SIMMONS, D. C. 1980. Review of the Florida spiny lobster resource. Fisheries 5(4): 37–42.

SIMS, H. W. JR., AND R. M. INGLE. 1967. Caribbean recruitment of Florida's spiny lobster population. Q. J. Fla. Acad. Sci. 29: 207–242.

SMITH, F. G. W. 1948. The spiny lobster industry of the Caribbean and Florida. Caribb. Res. Counc. Fish. Ser. Ser. 3: 49 p.

SUTCLIFFE, W. H. 1952. Some observations on the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. Proc. Gulf Caribb. Fish. Inst. 4: 64–69.

1953. Further observations on the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. J. Mar. Res. 12: 173–183.

1957. Observations on the growth rate of the immature Bermuda spiny lobster, *Panulirus argus*. Ecology 38: 526–529.

SWEAT, D. E. 1968. Growth and tagging studies on *Panulirus argus* (Latreille) in the Florida Keys. Fla. Board Conserv. Mar. Res. Lab. Tech. Ser. 57: 30 p.

WARNER, R. E., C. L. COMBS, AND D. R. GREGORY, JR. 1977. Biological studies of the spiny lobster, *Panulirus argus* (Decapoda: Palinuridae) in south Florida. Proc. Gulf Caribb. Fish. Inst. 29: 166–183.

WAUGH, G. T. 1981. Management of juvenile spiny lobster (*Panulirus argus*) based on estimated biological parameters from Grand Bahama Island, Bahamas. Proc. Gulf Caribb. Fish. Inst. 33: 271–289.

WEBER, D. 1968. Report to the Government of British Honduras (Belize) on investigations into marine fisheries, particularly spiny lobsters and shrimp resources. Rep. FAO/UNDP(TA)2541: 28 p.

WITHAM, R. R., R. M. INGLE, AND E. A. JOYCE, JR. 1968. Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. Fla. Board Conserv. Mar. Lab. Tech. Ser. 53: 31 p.

YANG, M. C. K., AND B. OBERT. 1978. Selected statistical analyses of Key West spiny lobster data, p. 4–7. *In* R. E. Warner [ed.] Spiny lobster research review; proceedings of a conference held December 16, 1976 in Key West, Florida. Fla. Sea Grant Tech. Pap. 4.

ZUBOY, J. R. 1980. The Delphi technique: a potential methodology for evaluating recreational fisheries. U.S. Dep. Commer. NOAA Tech. Memo. NMFS-SEFC-19: 25 p.

ZUBOY, J. R., A. C. JONES, AND T. J. COSTELLO. 1980. Lobster fishery management under the Fishery Conservation and Management Act. Fisheries 5(4): 50–52.

# Review of the Fishery for and Biology of the Cape Rock Lobster *Jasus lalandii* with Notes on Larval Recruitment

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The South African fishery for the rock lobster *Jasus lalandii* currently yields about 3800 metric tons (8.4 million animals) of which more than 90% are males. Males grow much faster than females, and a size limit which is fairly large in relation to the size and age at maturity protects females from exploitation for most of their lifespans, thereby ensuring a high level of larval production from the population. Exploitation rates in the fishery are controlled by means of quotas on fishing companies, as well as catch limits on individual fishing grounds. Quotas are reassessed annually to maintain instantaneous fishing mortality rates of approximately 0.3 on all grounds. Catch rates on most grounds have been increasing since area catch limits were introduced in 1980, and seasonal averages now vary between 4 and 12 kg·trap-day$^{-1}$. Although annual indices of puerulus larval recruitment are not available, and the stock–recruitment relationship is unknown, it appears that relatively stable yields can be maintained despite fluctuations in puerulus recruitment. Density-dependent regulatory mechanisms operative in juvenile and young adult stages tend to dampen large variations in the numbers of adults entering the fishable size range each year. Variations in puerulus recruitment are likely to result from changes in the paths and velocities of extensive offshore currents which eventually return larvae toward the coast of South Africa after many months of pelagic existence.

La pêche en Afrique du Sud de la langouste *Jasus lalandii* rapporte environ 3 800 tonnes métriques (8,4 millions d'individus) dont plus de 90 % sont des mâles. Les mâles croissent beaucoup plus vite que les femelles et une limite de taille qui est assez élevée par rapport à la taille et à l'âge atteint à la maturité protège les femelles contre l'exploitation pendant la majeure partie de leur vie, assurant ainsi un niveau élevé de production de larves dans la population. Les taux d'exploitation pour la pêche sont contrôlés au moyen de contingents imposés aux compagnies de pêche de même qu'au moyen de limites de prises pour chacun des lieux de pêche. Les contingents sont réévalués chaque année pour maintenir les taux instantanés de mortalité due à la pêche à environ 0,3 sur tous les lieux de pêche. Les taux de capture sur la plupart des lieux de pêche ont augmenté depuis que les limites de prises dans les secteurs ont été introduites en 1980 et les moyennes saisonnières varient maintenant entre 4 et 12 kg par jour de trappe. Bien que les indices annuels du recrutement des larves puerulus ne soient pas disponibles, et que l'on ne connaisse pas la relation entre le recrutement et les stocks, il semble que des rendements relativement stables peuvent être maintenus en dépit de fluctuations dans le recrutement des puerulus. Des mécanismes de régulation dépendant de la densité opératoires aux stades des juvéniles et des jeunes adultes ont tendance à amortir les grandes variations dans le nombre d'adultes qui entrent chaque année dans la catégorie des tailles exploitables. Les variations dans le recrutement des larves puerulus résultent probablement de changements dans les trajectoires et les vitesses du courant du grand large qui retournent éventuellement les larves vers la côte de l'Afrique du Sud après de nombreux mois d'existence pélagique.

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The rock lobster *Jasus lalandii* is one of seven species of the genus *Jasus* occurring in the Southern Hemisphere. *Jasus lalandii* ranges in distribution from about 23°S near Walvis Bay in Namibia to about 28°E near East London in the Cape Province of South Africa. Commercial densities are encountered only along the west coast, from about 25°S in Namibia to Cape Point just south of Cape Town (34°22′S).

The lengthy coastline, together with the high productivity of the Benguela upwelling system, enables this region of southern Africa to produce the world's largest yield of any *Jasus* species, with current landings of approximately 5600 metric tons (t). The annual catch from South African waters alone is approximately 3800 t at present, or some 8.4 million animals, of which 90–99% are males (Table 1). Adult females grow much more slowly than adult males, and the minimum size limit of 89 mm carapace length protects females from exploitation for most of their lifespans. Because the fishery is directed mainly at males, a high level of egg and larval production is maintained by the female population.

In this paper, the fishery for *J. lalandii* in South Africa is reviewed and management measures described. Biological information which is relevant to the management of the fishery is summarized, and hypotheses are developed regarding possible larval dispersal and recruitment mechanisms. The paper illustrates how effective management can be achieved, despite a current lack of detailed knowledge of puerulus settlement rates and variations in year-class strengths of juvenile lobsters.

## The Fishery

### Gear, Vessels, and Grounds

The West Coast region is divided into eight fishing grounds, shown in Fig. 1 (areas 1–8). In some areas, the traditional method of catching rock lobsters by means of hand-hauled baited hoopnets persists, although traps have come into in-

TABLE 1. Mean percentage of males in commercial catches of *J. lalandii* on five fishing grounds, 1980–81 to 1984–85. Mean number sampled per season shown in parentheses.

| Area (gear) | Mean % (1980–81 to 1984–85) | Range |
|---|---|---|
| Cape Peninsula | | |
| Traps | 99 (7736) | 99–99 |
| Dassen Island | | |
| Traps | 99 (4598) | 98–99 |
| Saldanha Bay | | |
| Traps | 90 (7358) | 86–91 |
| Hoopnets | 89 (2865) | 85–96 |
| Elands Bay | | |
| Traps | 99 (2905) | 98–99 |
| Hoopnets | 96 (3692) | 93–98 |
| Lambert's Bay | | |
| Traps | 94 (8096) | 92–97 |
| Hoopnets | 90 (3222) | 88–95 |

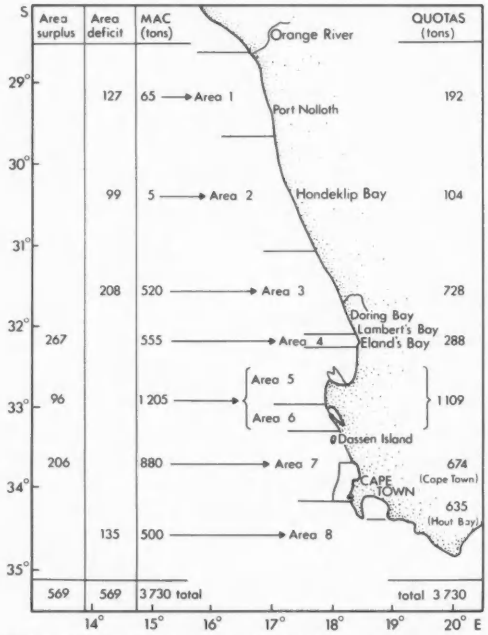


FIG. 1. Rock lobster fishing grounds off the Cape west coast (areas 1–8) showing quotas in relation to maximum allowable catches (MACs) per fishing ground.

creasingly greater use since 1970. Traps have large metal rectangular frames covered with polyethylene netting and are baited with fish (usually hake heads or horse mackerel). Newman and Pollock (1969) found traps to be approximately 2.5 times as efficient as hoopnets on southern grounds.

At present, 239 inboard motor vessels and some 1000 dinghies are licensed to fish for rock lobsters. Trap-fishing vessels, varying from about 6 to 14 m in length, deploy up to 80 traps and fish depths to about 80 m. Dinghies, which either operate independently from the shore or are towed or carried by inboard motor vessels, generally operate close inshore, at depths rarely exceeding 25 m.

TABLE 2. Annual landings and quotas of west coast rock lobster (converted to metric tons whole mass from factory production (tail weight) statistics prior to 1979).

| Season or period | Annual landings (t whole mass) | Quotas (t whole mass) |
|---|---|---|
| 1940–50 | ~7 300 annually | — |
| 1950–60 | ~10 640 annually | 11 000 |
| 1961–65 | ~10 370 annually | 10 400 |
| 1966 | 9 223 | 10 400 |
| 1967 | 7 100 | 10 400 |
| 1968 | 6 200 | 10 400 |
| 1969–70 | 5 900 | 7 840 |
| 1970–71 | 5 600 | 5 513 |
| 1971–72 | 5 290 | 5 294 |
| 1972–73 | 5 541 | 5 542 |
| 1973–74 | 5 722 | 5 722 |
| 1974–75 | 6 288 | 6 288 |
| 1975–76 | 6 297 | 6 297 |
| 1976–77 | 6 297 | 6 297 |
| 1977–78 | 6 297 | 6 297 |
| 1978–79 | 5 352 | 5 352 |
| 1979–80 | 5 352 | 5 643 |
| 1980–81 | 4 548 | 4 796 |
| 1981–82 | 3 700 | 3 700 |
| 1982–83 | 3 700 | 3 700 |
| 1983–84 | 3 730 | 3 730 |
| 1984–85 | 3 730 | 3 730 |
| 1985–86 | 3 805 | 3 805 |

## Historical Development

Commercial exploitation of *J. lalandii* commenced in the late nineteenth century and expanded during the early twentieth century, eventually levelling off at a catch of about 10 000 to 11 000 t, a level maintained from about 1950 to 1965 (Table 2). Fishing effort rose during this period as more vessels entered the fishery and ventured further from their home ports in search of better-yielding areas.

A minimum size limit of 89 mm carapace length was enforced from 1933 onwards, and a tail-mass production quota was introduced in 1946 to control catches destined for the export market.

Despite these measures, a decline in catches took place during the late 1960s, and quotas could not be filled for the first time in many years. Although detailed catch statistics by area are not available before 1970, available data show that the decline was particularly severe in the northern areas (areas 1 and 2 in Fig. 1) where virtually uncontrolled exploitation had taken place at a reduced minimum size limit of 76 mm after 1959 (Pollock 1982). In 1970, the production quota was reduced to the tail-mass equivalent of about 5513 t (to cover both export and local market production), divided amongst 34 quota-holding companies. At the same time, the size limit in areas 1 and 2 was again set at 89 mm.

Since 1970, catches have varied directly in accordance with quota levels set, which were increased gradually from 5290 t in 1971 to 6297 t in 1975. Changes in the fishery since 1975 are discussed in the next section. Other management measures which have been enforced from a very early period are a prohibition on the possession of berried females or soft-shelled lobsters, a winter closed season for fishing (at present from 1 July to 31 October in areas 1–6 and from 1 July to 14 November in areas 7 and 8), and a bag limit of five lobsters per day for amateur fishermen.

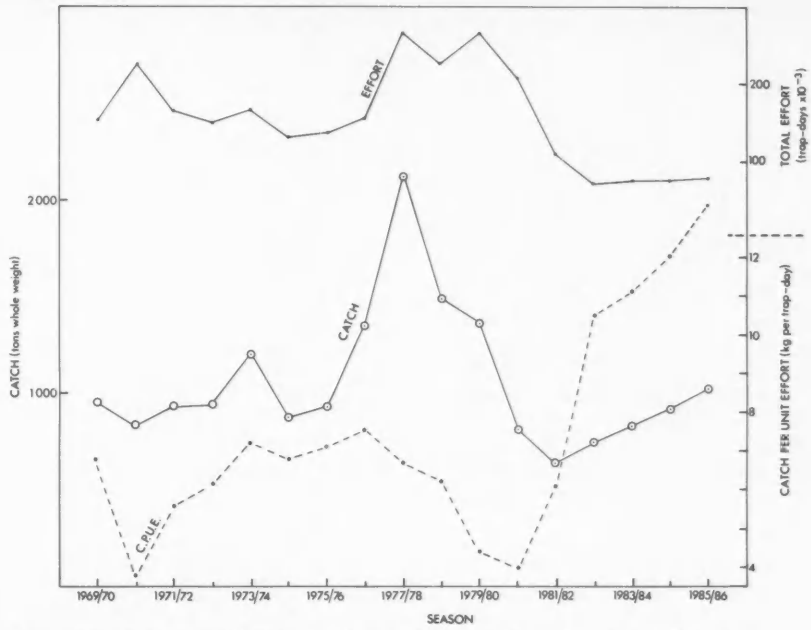


FIG. 2. Trends in catch, effort, and catch per unit effort at Dassen Island over 17 seasons.

## Current Management

Prior to 1980, movement of vessels from one fishing ground to another was not restricted in any way, but despite this, most vessels tended to fish on home grounds reasonably close to offloading points and quota-holding factories. However, in 1978 a marked shift in fishing effort commenced, when large vessels from northern and central areas left their traditional grounds in areas 3 and 4 and moved onto grounds further south, particularly Dassen Island (area 7 in Fig. 1). This movement was caused by a sudden decline in availability of rock lobsters in the Lambert's Bay area (area 3) in the 1977–78 fishing season, and the resulting shift in fishing effort led to a steep increase in catch and effort at Dassen Island, followed by a decline in catch per unit effort (CPUE) at this important southern fishing ground.

In response to the perceived threat of overfishing at Dassen Island, the industry agreed to impose a catch ceiling of 780 t for the 1980–81 fishing season. This step led to the formation of an association representing all companies and fishermen along the whole coast, and the concept of imposing maximum allowable catches (MACs) on all fishing grounds became generally accepted during the following fishing season. At about the same time, a whole lobster (landed mass) quota was introduced to replace the tail-mass production quota system, and official scales were installed at all 13 landing points to control quotas effectively.

MACs are now determined annually for each of the eight fishing grounds. The sum of MACs determines the total quota which is divided among 38 companies on a fixed percentage basis. Because company quotas in some areas are not in balance with the present-day yields or MACs of local fishing grounds, movement of vessels from areas with MAC shortfalls to areas with surplus MAC is arranged in advance of each fishing season by the association. Area MACs and company quotas summed by area are shown in Fig. 1, based on the 1984–85 season. It is quite clear that company quotas in areas

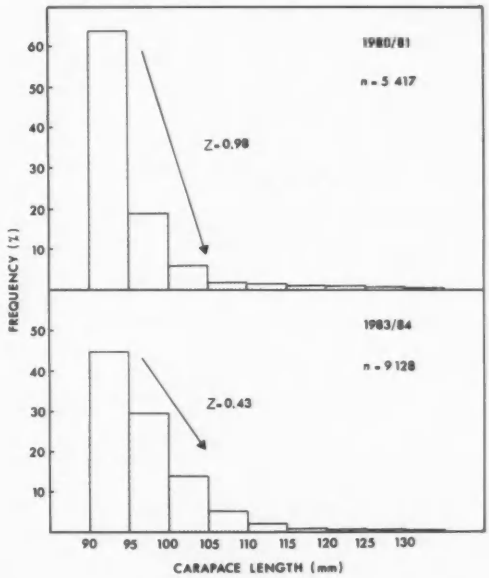


FIG. 3. Percentage size frequency distribution of commercial catches of male rock lobsters at Dassen Island in 1980–81 and 1983–84.

1 and 2 are much higher than local MACs so that most of their quotas have to be filled from southern grounds. The responsibility of ensuring that MACs are adhered to is left to the industry itself, under the auspices of the association. Each MAC has a ±7.5% flexibility to make the system more manageable.

The effects of MAC control over the stock at Dassen Island are illustrated in Fig. 2. The graph displays total catch, total effort, and CPUE from 1969 to 1985. A maximum sustainable

TABLE 3. Mean moult increments per size–class of male rock lobsters on three fishing grounds and of males and females at Robben Island sanctuary near Cape Town. Data from Pollock and Beyers (1981) and Pollock (1978). Number of observations in parentheses.

| | Males | | | Robben Island | |
|---|---|---|---|---|---|
| Size-class (mm) | Cape Peninsula | Dassen Island | Lambert's Bay | Males | Females |
| 70–79 | 4.7 (158) | 4.4 (152) | — | 6.3 (31) | 1.4 (18) |
| 80–89 | 3.8 (370) | 4.4 (387) | 4.8 (164) | 6.9 (58) | 0.7 (13) |
| 90–99 | 3.0 (247) | 4.5 (204) | 4.2 (132) | 8.0 (29) | 0.7 (5) |
| 100–109 | 2.4 (31) | 4.2 (41) | 2.9 (37) | 8.2 (18) | 0.3 (1) |

yield of approximately 800–1000 t had been estimated from tagging during the early 1970s (Newman 1973). Catches rose to over 2000 t during 1977–78, when the influx of fishing effort took place from further north. During the period 1977–78 to 1980–81, CPUE declined fairly rapidly. Catch limitations were introduced in 1980–81 and have been increased gradually since 1982, while CPUE has recovered from a low of about 4 kg·trap-day$^{-1}$ to over 12 kg·trap-day$^{-1}$ at present.

The size compositions of males in commercial catches at Dassen Island for 1980–1981 and 1983–84 are compared in Fig. 3. Estimates of total mortality, $Z$, based on available growth data were 0.98 and 0.43 in the two periods. If natural mortality, $M$, is assumed to be constant at 0.1, this indicates $F$ rates of 0.88 and 0.33, respectively, illustrating that fishing mortality has been reduced appreciably.

## Life History and Recruitment

Adult females moult annually, usually between April and June, and mating and oviposition take place shortly thereafter (Heydorn 1965, 1969; Newman and Pollock 1971, 1974a).

Recent studies by C. J. de B. Beyers and P. C. Goosen (in prep.) have shown that fecundity varies regionally in the Cape, with fewer eggs produced by females in areas where growth rates are retarded, that is, in the northern Port Nolloth area, and also at Olifantsbos, on the Cape Peninsula fishing ground. In the remaining areas, fecundity is described by the relationship

$$y = 4507.3x - 210\,284$$

where $y$ = number of eggs and $x$ = carapace length (millimetres).

Most mature females are in berry from July to late October each year and release their larvae while located close inshore. Peak hatching in October–November may be synchronized with the onset of strong southeasterly winds which induce upwelling at this time of the year. Upwelling tends to shift newly hatched phyllosoma larvae in the surface layers rapidly northwards and offshore by means of geostrophic currents and Ekman drift (Shannon 1985).

The larval cycle of *J. lalandii*, like that of most other palinurid species, remains enigmatical, and various hypotheses can be put forward to explain possible return mechanisms of late-stage larvae, as will be discussed later. What is known with certainty is that puerulus larvae are found inshore in greatest numbers between December and April, and settling generally takes place in depths shallower than 10 m (Pollock 1973). This suggests a minimum larval duration, including the puerulus stage, of 14–18 mo from hatching.

Juvenile rock lobsters of both sexes moult several times per year, the frequency decreasing with increasing size. Moult increments, expressed as a percentage of premoult carapace length, also decline with increasing size. Lobsters of each sex attain a carapace length of about 60 mm 4 yr after they settle as puerulus larvae, and females reach sexual maturity about 5 yr after settlement (Pollock 1973).

The size at which females mature varies slightly, both between and within certain fishing grounds such as Dassen Island and the Cape Peninsula (Newman and Pollock 1974a). However, a noticeably smaller size at maturity has been recorded by Pollock and Beyers (1981) for females in Namibian waters, and more recently in the Port Nolloth region as well. Figure 4 shows a series of maturity curves for different areas, with sizes at 50% maturity listed. Data are based on the presence of ovigerous setae. Sample sizes were large, ranging from 647 to 1725 on the three southern grounds to 1618 at Port Nolloth and 146 at Beverley Hills, Namibia. It is evident that size at maturity declines appreciably to the north, a phenomenon which is unrelated to water temperature, since the whole coastline is equally influenced by the cool Benguela upwelling system.

As in the case of adult females, adult males also normally moult once per year, in late spring or early summer. Males first attain maturity at about 60–65 mm in size (Heydorn 1965). Timing of moulting varies with latitude, moulting taking place progressively later towards the south. September is the peak month in areas 1 and 2 and October in areas 3 and 4, whereas in areas 7 and 8, November and early December are peak periods for male moulting (Pollock 1978). In general, adult males moult about 6 mo earlier than adult females, so that when mating takes place males are hard-shelled and females are in a soft-shelled condition.

Moult increments of adult males and females normally decline with increasing size of animal, but are generally much smaller in females than in males. As a result of differential growth between the sexes, males reach legal size (89 mm) at about 7–11 yr of age, whereas females exceed 20 yr of age at the same size (Pollock 1978). Growth increments are shown in Table 3 for males from some southern fishing grounds, as well as for males and females at Robben Island, a sanctuary near Cape Town.

Growth rates of males vary regionally, with small increments recorded from northern areas in the Cape and in Namibia (Pollock and Beyers 1981), but annual variations are also known to occur, and differences have been recorded even within localized areas (Newman and Pollock 1974b; Pollock 1978, 1982; Pollock et al. 1982). In many of these cases, differences in adult growth rates have been ascribed to differences in densities of rock lobsters in relation to available food supplies, suggesting that density-dependent regulation of growth rates is operative in adults as well as in juveniles.

An instantaneous natural mortality ($M$) of 0.1 has been calculated by Pollock (1978) for adult males at Robben Island

TABLE 4. Catches of phyllosoma and puerulus larvae by depth during day and night hauls off the Cape Peninsula during August 1983 and August 1984 surveys.

| Depth range of oblique tow (m) | Time | No. of phyllosoma larvae | No. of puerulus larvae | Surface temp. (°C) | Temp. at greatest depth (°C) |
|---|---|---|---|---|---|
| *West of Cape Peninsula, 1015 m depth, 22–23 August 1983* | | | | | |
| 100–10 | 20:25–21:25 | 27 | 0 | 15.0 | 14.8 |
| 200–100 | 22:36–23:36 | 1 | 0 | 15.2 | 11.7 |
| 200–100 | 08:00–09:00 | 5 | 2 | 15.2 | 11.6 |
| 300–200 | 09:30–10:30 | 3 | 1 | 15.2 | 9.8 |
| 400–300 | 11:30–12:30 | 0 | 0 | 15.0 | 8.0 |
| 300–200 | 13:00–14:00 | 16 | 2 | 15.2 | 10.1 |
| 150–10 | 15:00–16:00 | 8 | 0 | 15.2 | 12.6 |
| 250–150 | 16:30–17:30 | 6 | 0 | 15.2 | 10.9 |
| *West of Cape Peninsula, 2850 m depth, 23 August 1984* | | | | | |
| 120–20 | 22:50–23:50 | 10 | 0 | 15.1 | 13.6 |
| 200–100 | 11:30–12:30 | 7 | 0 | 15.3 | 10.4 |
| 300–200 | 13:20–14:20 | 4 | 0 | 15.3 | 9.9 |
| 400–300 | 15:00–16:00 | 0 | 0 | 15.4 | 8.1 |

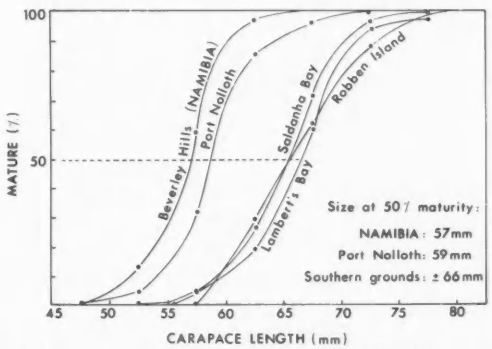


FIG. 4. Size at maturity curves for female *J. lalandii* in southern Namibia, Port Nolloth, and three fishing grounds further south.

sanctuary near Cape Town, and values between 0.05 and 0.2 have been used in yield-per-recruit calculations (Newman and Pollock 1977). Low values such as these are to be expected for adults because predators such as octopus and dogshark are not abundant, and both are removed as by-catches in the rock lobster trap fishery. Although adult seals (*Arctocephalus pusillus*) rarely feed on rock lobsters (Rand 1959; Heydorn 1969), small *J. lalandii* are commonly ingested by seal pups less than 1 yr old. Cannibalism is also likely to be an important source of mortality on small juvenile lobsters in overcrowded situations, where shelter may be a limiting factor.

Movement of adult rock lobsters between fishing grounds is minimal, as deduced from the results of numerous intensive tagging programmes conducted in different areas of the coast during the past 15 yr. Migratory movements, combined with partial segregation of the sexes, occur in some areas, but these consist of inshore migrations associated with moulting and breeding cycles (Pollock 1982; Pollock et al. 1982). At Elands Bay (area 4), rock lobsters have been found to move inshore and offshore in response to seasonal incursions of oxygen-depleted bottom waters (Newman and Pollock 1971). In this area of the coast, and in the adjacent St. Helena Bay, near-seabed oxygen concentrations regularly decline in summer and autumn due to decaying particulate matter in bottom waters, the result of extremely high primary production rates in summer (Pollock and Bailey 1986).

TABLE 5. Relative egg production per size-class of females at Robben Island sanctuary. Size and maturity data from Pollock (1982); fecundity: $y = 4507.3x - 210\,284$ (C. J. de B. Beyers and P. C. Goosen, in prep.).

| Size-class (mm) | Frequency of mature females | Frequency × fecundity ($\times 10^{-3}$) | Percentage egg production |
|---|---|---|---|
| 60–64 | 63 | 4 498 | 2.0 |
| 65–69 | 330 | 31 006 | 13.8 |
| 70–74 | 504 | 58 713 | 26.2 |
| 75–79 | 387 | 53 805 | 24.0 |
| 80–84 | 217 | 35 060 | 15.6 |
| 85–89 | 118 | 21 724 | 9.7 |
| 90–94 | 54 | 11 159 | 5.0 |
| 95–99 | 24 | 5 500 | 2.5 |
| 100–104 | 5 | 1 259 | 0.6 |
| 105–109 | 4 | 1 097 | 0.5 |
| 110–114 | 1 | 297 | 0.1 |
| Total | 2136 | 224 118 | 100.0 |

Further north, in the Port Nolloth and Hondeklip Bay areas, as well as along the Namibian coast, oxygen-depleted bottom waters appear to restrict rock lobsters to a narrow fringe along the coast for the greater part of the year (Pollock 1982). Animals are rarely, if ever, captured deeper than about 20 m in this region. D. E. Pollock and L. V. Shannon (in prep.) have suggested that yields in areas 1 and 2, as well as in Namibia, have been greatly influenced by oxygen-depleted bottom waters which are thought to have intensified after about 1960 in the northern regions of the Benguela system. The reduced habitat available to adult lobsters has led to overcrowding in the shallow kelp beds, with pronounced density-dependent effects on growth and mortality, as well as a diminution in the size at maturity of females.

Although adults on different fishing grounds are treated as distinct units for management purposes, it is not suggested that these units are discrete with respect to larval recruitment. As mentioned earlier, the teleplanic phyllosoma larvae (Scheltema

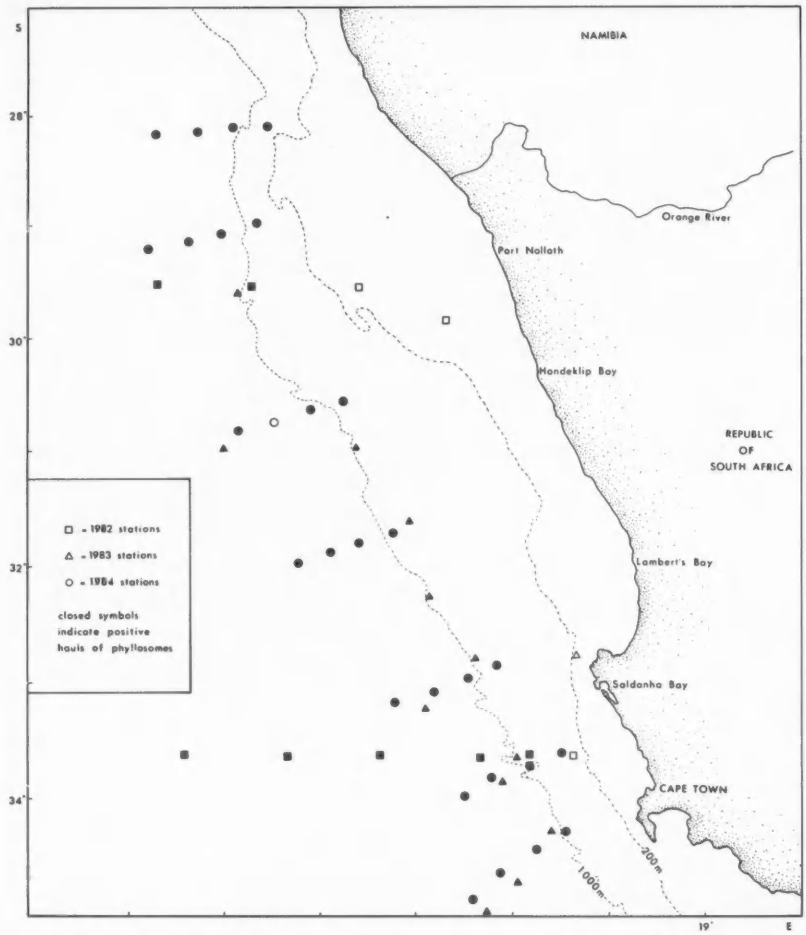


FIG. 5. RMT-net station positions during phyllosoma larval surveys of August 1982, 1983, and 1984.

1971) of *J. lalandii* spend an extensive time drifting far offshore, having been found as far west as 13°30′E, some 460 km offshore, during recent surveys (SFRI, unpubl. data). Lazarus (1967) examined phyllosoma larvae caught in vertical plankton hauls at 95 stations sampled monthly off the southwestern Cape between 1961 and 1964 and found large numbers of early stage larvae at nearshore stations shortly after peak hatching. Mid-stages were very much less common, while late stages (his stages IX–XIII) were found only at stations well offshore, extending at least 300 km seaward, and were mainly present during the winter months. Silberbauer (1971) subsequently revized Lazarus' 13 phyllosoma stages to 11 stages in total.

An intensive ichthyoplankton survey conducted monthly from August 1977 to August 1978 at about 120 stations inshore of the 1000-m isobath off the southwestern Cape failed to catch any late-stage (VI–XI) larvae. More recently, during July 1982, a series of plankton hauls were made at 49 stations between the coast and the 500- to 1000-m isobath (shelf-break), making use of a large RMT-8 net (a rectangular midwater trawl with mouth area of 8 $m^2$). Late-stage phyllosoma larvae were only encountered at three stations, and these were all near the shelf-break. Sufficient evidence was thus available to conclude the late-stage larvae were not to be found inshore of the shelf-break in any significant quantities. Accordingly, a series of research cruises were designed in August of 1982, 1983, and 1984 to investigate the behaviour and distribution of phyllosoma larvae at and beyond the shelf-break during midwinter when late stages were expected to be most abundant. Station positions on the three surveys are shown in Fig. 5.

Results from the 1982 survey suggested that phyllosoma larvae were concentrated in the upper 100 m during the hours of darkness, so during the August 1983 and 1984 surveys, hauls were conducted as standard 1-h oblique tows at night between 120 and 20 m at a towing speed of 2.5–3 knots. A temperature versus depth profile was recorded during each tow. The RMT-8 net was lowered in the closed mode, opened at 120 m, raised gradually while hauling up to 20 m, and then closed and retrieved. Phyllosoma larvae were removed from the catch, preserved, and later identified. *Jasus* larvae were staged according to Silberbauer (1971) and measured (cephalic shield width).

A number of additional experimental hauls were made in areas of high larval densities to compare depth distributions of larvae by day and by night. The results of these are summarized

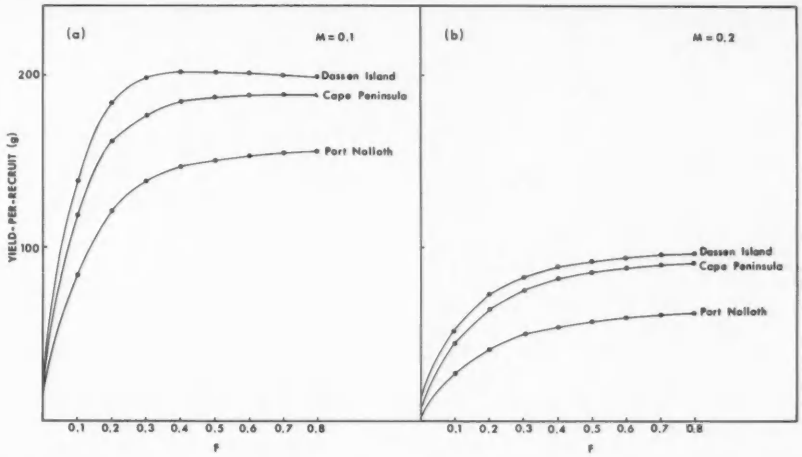


FIG. 6. Yield-per-recruit curves for male *J. lalandii* on three fishing grounds for (a) $M = 0.1$ and (b) $M = 0.2$.

in Table 4, from which it was concluded that at night the larvae (mainly stages X and XI) were almost exclusively located in the upper 100 m, while during the day they descended to depths not exceeding 300 m.

From the temperature–depth profiles recorded, it was evident that larvae moved through a significant temperature gradient during the course of their diel migrations. A thermocline, varying from depths of 100 to 140 m, separated the oceanic surface water of 14–16°C from cooler underlying waters with temperatures dropping to about 10–12°C at depths of 200–300 m on the August 1983 and August 1984 surveys. From temperature and salinity characteristics, measured by CTD, the water mass below the thermocline was identified as South Atlantic Central water extending to depths of 500–600 m.

Figure 5 shows that phyllosoma larvae were found at virtually all stations sampled outside the shelf. During the August 1984 survey, which was the most comprehensive of the three, a total of 212 phyllosoma larvae were caught, of which 185 larvae were *Jasus* and of these 183 were late stages VI–XI. A total of only 10 puerulus larvae were caught, mainly at the innermost stations of the 111-km-wide transects.

On all three surveys, relatively few puerulus larvae were caught, but their presence near the shelf-break, together with numbers of final-stage XI larvae, and earlier proof that late and final stages were absent from waters closer inshore, suggests that final-stage phyllosoma larvae complete their metamorphosis into the puerulus stage in waters close to or overlying the shelf-break. It follows that puerulus larvae have to cross the continental shelf, which varies in width from about 180 km in the north to about 50 km in the south, before they settle in shallow water along the coast.

Because one objective of this paper was to examine possible types of stock–recruitment relationships of *J. lalandii*, it is instructive to try to assess changes in egg production which may have resulted from decades of continuous fishing pressure directed at adults larger than 89 mm. Some indication of the level of egg and larval production by female lobsters in early years (when exploitation was still minimal) can be gauged from a calculation of egg production by different size-classes of females collected in a sanctuary population. The Robben Island sanctuary population can be viewed as a preexploitation population of *J. lalandii*. Relative egg production per size-class was calculated from female size distribution (sampled by divers), the percentage mature in each size-class, and the average fecundity of females per size-class (Table 5).

TABLE 6. Catch per unit effort of traps for six fishing grounds, 1969–70 to 1984–85.

| Season | CPUE of traps (kg·trap-day$^{-1}$) by area | | | | | |
|---|---|---|---|---|---|---|
| | Area 3 | Area 4 | Area 5 | Area 6 | Area 7 | Area 8 |
| 1974–75 | — | — | 7.0 | 6.0 | 6.7 | 10.5 |
| 1975–76 | 10.5 | — | 5.2 | 6.6 | 6.9 | 8.4 |
| 1976–77 | 3.1 | — | 3.9 | 10.0 | 8.0 | 8.2 |
| 1977–78 | 2.8 | 3.1 | 3.6 | 6.1 | 6.7 | 4.0 |
| 1978–79 | 2.1 | 2.5 | 5.3 | 6.6 | 5.8 | 5.7 |
| 1979–80 | 1.5 | 2.2 | 4.3 | 5.3 | 4.3 | 6.8 |
| 1980–81 | 1.8 | 2.3 | 3.4 | 4.2 | 3.9 | 3.7 |
| 1981–82 | 2.3 | 6.3 | 4.7 | 4.5 | 6.0 | 3.8 |
| 1982–83 | 3.5 | 9.9 | 4.1 | 4.3 | 10.5 | 4.6 |
| 1983–84 | 5.6 | 8.2 | 5.1 | 4.2 | 11.2 | 6.0 |
| 1984–85 | 3.7 | 6.7 | 6.8 | 4.9 | 12.1 | 7.6 |

Table 5 shows that egg production from females larger than 90 mm (approximately the minimum size limit of 89 mm) is only about 9% of the total egg production from all size-classes combined. Therefore, even on typical fishing grounds, where animals larger than 89 mm are today much reduced in abundance, egg production is not likely to be less than about 90% of preexploitation levels (assuming that the abundance of sub-legals has not changed).

## Research

Three sets of information are used for monitoring seasonal abundance and rates of exploitation of rock lobsters on the fishing grounds. These are CPUE, commercial catch size composition, and tagging results.

Considerable emphasis is placed on yield-per-recruit analyses to manage the fishery under the quota system. Since male

rock lobsters constitute more than 90% of commercial catches in nearly all areas of the coast (Table 1), and growth rates of males are documented in most areas, a set of yield-per-recruit curves for males has been constructed which encompasses the range of growth rates occurring in the field. For computation of yield-per-recruit, use is made of a Thompson and Bell model in which annual carapace lengths are entered, calculated directly from actual growth data. To compare yield-per-recruit curves between areas with different growth rates, the model assumes an initial input of 1000 male recruits at 60 mm carapace length, i.e. the same initial number of juvenile recruits per unit length of coastline for each area.

Figure 6 shows yield-per-recruit curves generated at natural mortality rates ($M$) of 0.1 and 0.2. Relative values of yield-per-recruit are considerably reduced in an area with slow growth, typified by the Port Nolloth curves, and values are very much reduced at the higher mortality rate (Fig. 6b). This is largely the result of relatively fewer survivors attaining the minimum size limit of 89 mm before fishing commences.

In general, although the curves differ in their relative heights, their shapes (especially for $M = 0.1$) illustrate that maximum yields will be sustained with minimum fishing effort by restricting fishing mortality to approximately $F = 0.3$.

Current management strategy aims at preventing growth overfishing on all grounds, at maintaining high rates of economic return (i.e. high CPUE), and at buffering the adverse effects of poorer-than-average recruitment on catches by maintaining a number of different age-classes in the legal-sized population. This is effected by adjusting MACs to the level which generates a fishing mortality rate of approximately 0.3.

Table 6 lists mean seasonal values of trap CPUE for areas 3–8 (no trap-fishing takes place in areas 1 and 2) over the past 11 seasons. It is evident that catch rates (CPUE) have increased on virtually all fishing grounds since MAC control was instituted in 1980–81. The marked increase in CPUE in area 4 is also thought to be largely the result of exceptionally good recruitment. In 1975 a discrete peak of sublegal-sized animals (modal size 67 mm carapace length) was recorded in samples collected randomly by divers at Elands Bay (Pollock 1978). Males from this cohort began entering the fishery in November 1981, 6 yr later, and they boosted catch rates dramatically for the next 3 yr. In 1984–85 there were signs of a downturn in CPUE in this area, as the dominant cohort had been reduced by fishing and natural mortality.

As mentioned earlier, concessions to pack lobsters smaller than 89 mm were first allowed in area 1 in 1959 when catches at Port Nolloth were declining (Pollock 1982). It was alleged at the time that lobsters there were a smaller "variety" than those further south. As described by Pollock (1982), catches at Port Nolloth were boosted for 2 or 3 yr after full official sanction was given for a 76-mm minimum size limit in 1963. A subsequent decline in catches prompted the authorities to reinstate the 89-mm size limit in 1970.

Despite reduced fishing effort in areas 1 and 2 since 1970, these areas have shown no signs of recovery, and catches have remained low. As mentioned earlier, growth rates are known to vary considerably amongst different grounds, and in theory it is possible that different minimum size limits on different grounds could optimize yields. In practice, this has been difficult to control, so that for convenience, a single size limit of 89 mm has been enforced since 1970. With the recently introduced system of MACs, it has been possible to introduce a smaller size limit of 75 mm in areas 1 and 2, on an experimental basis. This was initiated in the 1985–86 season, and tagging results to date (D. E. Pollock and P. A. Wickens, in prep.) have reaffirmed that growth is indeed retarded in this region. It is also suspected that the natural mortality rate (especially of sublegal-sized animals) is high, caused by overcrowding of adults and juveniles into a narrow subtidal fringe. As discussed earlier, the depth distribution of lobsters in these northern regions is strongly influenced by the presence of oxygen-deficient bottom waters further offshore.

## Discussion

A high level of egg production by female *J. lalandii* can be maintained even on heavily exploited fishing grounds. This is because the fishery is largely directed at males, the minimum size limit of 89 mm protecting mature females from exploitation for at least 15 yr before they become eligible for capture. With a high level of larval production guaranteed, the risk of recruitment failure caused by overfishing is considerably reduced in comparison with other fisheries where the age at first capture is low, sometimes even below the onset of sexual maturity of females.

Owing to the (assumed) relatively stable egg and larval production and a lack of detailed knowledge of annual variations in puerulus recruitment, it has not been possible to establish a stock–recruitment relationship for *J. lalandii*. Although recruitment of adults into the fishable stock apparently fluctuates from year to year in different areas, this is not likely to be directly related to fluctuations in parent stock size (i.e. egg production). Phyllosoma larvae are widely dispersed in offshore waters before the puerulus stage returns to the coast, so that it is likely that environmental effects on larval survival, e.g. variations in the paths and velocities of offshore currents, would influence the numbers of puerulus larvae recruiting onshore in any particular area of the coast. In any event, large upward fluctuations in annual recruitment of puerulus larvae are likely to be "damped" by the ceiling imposed by the carrying capacity (food, shelter) of the nearshore rocky areas in which settlement and subsequent growth take place. Density-dependent growth and mortality of older juveniles will also tend to further damp these fluctuations, since abnormally high densities should cause reduced growth and higher natural mortality in juvenile populations which are food limited or space limited. To some extent, the reverse would tend to take place when abnormally low settlement of puerulus larvae occurred.

Intuitively, one would expect a plot of "numbers of juvenile recruits versus egg production" to take the form of a flattened dome-shaped Ricker curve in which the right limb could be close to horizontal. This would imply that adequate recruitment could be maintained over a wide range of adult stock sizes. Geographic and temporal variations in puerulus recruitment are likely to be induced by environmental factors during the lengthy larval phase.

Despite a lack of detailed knowledge about variations in recruitment strength of puerulus larvae, or of subsequent juvenile year-classes, it has nonetheless been possible to manage the fishery for *J. lalandii* fairly effectively, particularly in recent years. The reason underlying this is probably because annual fluctuations in recruitment by growth into the legal size range each year tend to be damped by density-dependent mechanisms regulating the abundance of juvenile and young adult age-classes. In addition, with growth rates varying seasonally and amongst different fishing grounds, a variable mixture of

age-classes is probably entering the fishery each year, further reducing the dependence of the fishery on any single year-class. This is in marked contrast to several other major spiny lobster fisheries with a much lower age at first capture, in which the annual success of the fishery relies heavily on a single, intensively fished year-class which recruits into the legal size range each year. Examples of the latter are the Florida fishery for *Panulirus argus* (Davis 1980; Gregory et al. 1982) and the West Australian fishery for *P. cygnus* (Phillips et al. 1980; Hancock 1981).

As mentioned earlier, the mechanisms of larval transport remain problematical, not only for *J. lalandii*, but for palinurids in general. However, studies by Johnson (1960, 1974), Lesser (1978), Booth (1979, 1980), and Phillips et al. (1978, 1979), among others, have revealed certain features which appear to be common to the phyllosoma larval cycles of many of the palinurids. These may be summarized as follows.

(1) Hatching of eggs often takes place when current strengths are maximal, thereby ensuring rapid (offshore) dispersal (Phillips et al. 1979; this study), while in the case of shallow-water tropical palinurids, females often move to deep reef areas to spawn, as these habitats are usually more closely allied with longshore oceanic currents (Kanciruk and Herrnkind 1976; Davis 1977; Gregory et al. 1982).

(2) Larvae have been found great distances offshore, e.g. *P. cygnus* to 1500 km in the Indian Ocean (Phillips et al. 1979) and *P. penicillatus* and *P. gracilis* in the Pacific to some 3300–3700 km from their point of likely origin (Johnson 1974). If moulting can take place without change of form e.g. "mark-time" moulting (Gore 1985), development can be delayed considerably, thereby greatly extending potential larval life. This type of moulting is known to occur in scyllarid and panulirid phyllosomes, when food is severely limited.

(3) Larvae undergo progressively greater vertical diel migrations in their later stages (Rimmer and Phillips 1979). Most final-stage larvae only metamorphose into the puerulus stage when they reach the vicinity of the edge of the continental shelf, suggesting that recognition of a set of specific environmental cues may be a trigger for metamorphosis (Annala 1983).

(4) Puerulus larvae are mainly found over the shelf and closer inshore. Directional swimming ability is thought to take place, enabling puerulus larvae to cross the shelf and settle in suitable habitats close inshore (Phillips 1981; Sims and Ingle 1966; Witham et al. 1968; Little 1977).

Phillips (1981) has suggested two possible mechanisms for the coastward return of phyllosoma larvae of *P. cygnus*, namely via the large southeastern Indian Ocean gyre or via eddies imbedded within this larger system. Because of increasingly greater vertical migrations by mid- and later stages, he suggested that the return of these stages is facilitated by the larvae spending proportionately more time in subsurface waters which have a predominant easterly flow towards the west coast of Australia.

Off the South African coast, early stage phyllosoma larvae of *J. lalandii* are shifted rapidly northwards and offshore in near surface layers, which drift in a northwesterly direction, crossing the Walvis Ridge before heading towards St. Helena Island (15°58′S, 5°43′W), as part of the South Atlantic gyre. The offshore movement of surface Benguela waters is confirmed by the paths of satellite-tracked drogues released off Cape Town (Nelson and Hutchings 1983), as well as from drift-card returns released off the southwestern Cape and recovered at St. Helena Island (Shannon et al. 1973). The latter authors received recoveries from St. Helena Island, the coast of Brazil, and Isla da Trindade some 1160 km off the coast of Brazil and estimated mean current velocities in the gyre of about 16 $cm \cdot s^{-1}$. More recently, in 1977–78, P. A. Shelton (in prep.) released approximately 2400 drift cards each month for 12 mo off the southwestern Cape. Of the approximately 1300 cards recovered, about 5% were found at St. Helena Island, Isla da Trindade, and the coast of Brazil, the rest being recovered locally on Cape shores.

The Brazil current is the western boundary current of the South Atlantic. It diverges from the coast of Brazil south of Rio de Janeiro and merges with the general anticlockwise circulation of the South Atlantic.

The implication of this circulation pattern for the phyllosoma larvae of *J. lalandii* is that mechanisms must exist which enable larvae, which are initially entrained in the northwesterly offshore flow, to retard their movement, for example by entering eddy systems within the large South Atlantic gyre. Shannon (1985, p. 131) referred to "reversable and mesoscale gyres" centred some 900–1300 km off the Cape and Namibia, which might possibly retain some larvae within this southeastern sector of the Atlantic. However, their return toward the shelf-break region is not readily explained because no significant eastward flow, even at subsurface depths, has yet been demonstrated in this area, except in the extreme south at latitudes higher than about 33°S (Shannon 1985).

An alternative hypothesis is that larvae complete the whole South Atlantic gyre circuit before returning toward the Cape. This would imply that the larval life of *J. lalandii* is longer than previously supposed, since Shannon et al. (1973) have estimated a rotational period of the gyre of about 38 mo. A larval life of this duration is not inconceivable, considering that delayed development is a common feature in many decapod larvae, and that moulting without growth or change of form is a well-known type of larval ecdysis, especially in scyllarid and panulirid phyllosomas subjected to food deprivation (Gore 1985). It might also be found that Shannon et al. (1973) overestimated the mean circulation time, since pilot charts of the South Atlantic show mean current speeds of about 0.4–0.6 knots or approximately 21–31 $cm \cdot s^{-1}$ at the surface over most of the wind-driven circulation route. It is also noteworthy that Lutjeharms and Heydorn (1981) calculated mean current velocities varying from 20 to 23 $cm \cdot s^{-1}$ (in summer) to 33 $cm \cdot s^{-1}$ (in autumn and winter) in the eastward flowing current between about 36 and 40°S in the southeastern South Atlantic. These velocities were computed from the drift of three satellite-tracked buoys released in the vicinity of Tristan da Cunha and Gough Island in November 1978 and March 1979. All three buoys drifted eastwards, along the Subtropical Convergence, but changed to a more northerly route at about 10°E.

If most larvae of *J. lalandii* follow this route, they could return toward the southwestern coast of South Africa sometime between 1 and 2.5 yr after release, depending on the length of the route taken and current velocities at different times in different parts of the gyre.

Most larvae would tend to concentrate near the shelf-break in the south during winter when northward and coastal movement of southern Atlantic surface waters is maximal. Shannon et al. (1973) first deduced this movement from drift-card returns and noted that three subantarctic copepod species which are plentiful in the vicinity of the Subtropical Convergence make their appearance in offshore waters along the west coast

of South Africa during late winter and early spring, thereby confirming the northward drift of surface water from the Convergence towards South Africa during winter.

In conclusion, a circumoceanic route exists whereby larvae of *J. lalandii* might be returned to the coast of South Africa and Namibia, but use of the extensive South Atlantic gyre system implies a longer larval duration than was previously supposed.

Despite the still-present uncertainties about precise details of the larval return mechanisms, the variability of puerulus recruitment, and the year-class strengths of juvenile *J. lalandii*, the fishery as a whole appears to be relatively stable. It is evident that the fishery is not heavily dependent on a single year-class of recruits entering the legal size range each year, and the high age at first capture, combined with geographical and temporal variations in growth rates, leads to a mixture of recruiting year-classes. Maintaining fishing mortality rates at about 0.3 helps to optimize catch rates (CPUE) and retains a number of size- and age-classes in the fishable population, thereby buffering the adverse effects of below-average recruitment into the legal size range in any year.

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## References

ANNALA, J. H. 1983. New Zealand rock lobsters: biology and fishery. Occas. Publ. Fish. Res. Div. Minist. Agric. Fish. N.Z. 42: 36 p.

BOOTH, J. D. 1979. Settlement of the rock lobster, *Jasus edwardsii* (Decapoda: Palinuridae), at Castlepoint, New Zealand. N.Z. J. Mar. Freshwater Res. 13: 395–406.

1980. Larval recruitment studies. Catch '80. 7: 22–23.

DAVIS, G. E. 1977. Effects of recreational harvest on a spiny lobster, *Panulirus argus*, population. Bull. Mar. Sci. 27: 223–236.

1980. Spiny lobster series. Fisheries 5(4): 27–62.

GORE, R. H. 1985. Moulting and growth in decapod larvae, p. 1–65. *In* A. M. Wenner [ed.] Crustacean issues 2: Larval growth. A. A. Balkema, Rotterdam and Boston. 236 p.

GREGORY, D. R., R. F. LABISKY, AND C. L. COMBS. 1982. Reproductive dynamics of the spiny lobster *Panulirus argus* in South Florida. Trans. Am. Fish. Soc. 111: 575–584.

HANCOCK, D. A. 1981. Research for management of the rock lobster fishery of Western Australia. Proc. Gulf Caribb. Fish. Inst. (San Jose, Costa Rica). 3: 207–229.

HEYDORN, A. E. F. 1965. The rock lobster of the South African west coast *Jasus lalandii* (H. Milne-Edwards). 1. Notes on the reproductive biology and the determination of minimum size limits for commercial catches. Invest. Rep. Div. Sea Fish. S. Afr. 53: 32 p.

1969. The rock lobster of the South African west coast *Jasus lalandii* (H. Milne-Edwards). 2. Population studies, behaviour, reproduction, moulting, growth and migration. Investl. Rep. Div. Sea Fish. S. Afr. 71: 52 p.

JOHNSON, M. W. 1960. The offshore drift of larvae of the California spiny lobster, *Panulirus interruptus*. Calif. Coop. Oceanic Fish. Invest. 7: 147–161.

1974. On the dispersal of lobster larvae into the east Pacific barrier (Decapoda, Palinuridae). Fish. Bull. Natl. Mar. Fish. Serv. U.S. 72: 639–647.

KANCIRUK, P., AND W. F. HERRNKIND. 1976. Autumnal reproduction in *Panulirus argus* at Bimini, Bahamas. Bull. Mar. Sci. 26: 417–432.

LAZARUS, B. I. 1967. The occurrence of phyllosomata off the Cape with particular reference to *Jasus lalandii*. Investl. Rep. Div. Sea Fish. S. Afr. 63: 38 p.

LESSER, J. H. R. 1978. Phyllosoma larvae of *Jasus edwardsii* (Hutton) (Crustacea: Decapoda: Palinuridae) and their distribution off the east coast of the North Island, New Zealand. N.Z. J. Mar. Freshwater Res. 12: 357–370.

LITTLE, E. J. 1977. Observations on recruitment of postlarval spiny lobsters, *Panulirus argus*, to the South Florida Coast. Fla. Mar. Res. Publ. 29: 35 p.

LUTJEHARMS, J. R. E., AND A. E. F. HEYDORN. 1981. The rock lobster *Jasus tristani* on Vema Seamount: drifting buoys suggest a possible recruiting mechanism. Deep-Sea Res. 28A: 631–636.

NELSON, G., AND L. HUTCHINGS. 1983. The Benguela upwelling area. Prog. Oceanogr. 12: 333–356.

NEWMAN, G. G. 1973. Assessment and management of some marine stocks in Southern Africa. Ph.D. thesis, University of Stellenbosch, South Africa. 268 p.

NEWMAN, G. G., AND D. E. POLLOCK. 1969. The efficiency of rock lobster fishing gear. S. Afr. Shipp. News Fish. Ind. Rev. 24: 79–81.

1971. Biology and migration of rock lobster *Jasus lalandii* and their effect on availability at Elands Bay, South Africa. Investl. Rep. Div. Sea Fish. S. Afr. 94: 24 p.

1974a. Biological cycles, maturity and availability of rock lobster *Jasus lalandii* on two South African fishing grounds. Investl. Rep. Sea Fish. Branch S. Afr. 107: 16 p.

1974b. Growth of the rock lobster *Jasus lalandii* and its relationship to benthos. Mar. Biol. 24: 339–346.

1977. The population dynamics of rock lobster *Jasus lalandii* on two South African fishing grounds. Collect. Sci. Pap. Int. Comm. Southeast. Atl. Fish. 4: 175–187.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

PHILLIPS, B. F., P. A. BROWN, D. W. RIMMER, AND D. D. REID. 1979. Distribution and dispersal of the phyllosoma larvae of the western rock lobster *Panulirus cygnus* in the southeastern Indian Ocean. Aust. J. Mar. Freshwater Res. 30: 773–783.

PHILLIPS, B. F., G. R. MORGAN, AND C. M. AUSTIN. 1980. Synopsis of biological data on the western rock lobster *Panulirus cygnus* George, 1962. F.A.O. Fish. Synop. 128: 64 p.

PHILLIPS, B. F., D. W. RIMMER, AND D. D. REID. 1978. Ecological investigations of the late stage phyllosoma and puerulus larvae of the western rock lobster *Panulirus longipes cygnus*. Mar. Biol. 45: 347–357.

POLLOCK, D. E. 1973. Growth of juvenile rock lobster *Jasus lalandii* (H. Milne Edwards). Investl. Rep. Sea Fish. Branch S. Afr. 106: 16 p.

1978. Growth and production rates of the rock lobster *Jasus lalandii* (H. Milne Edwards). Ph.D. thesis, University of the Witwatersrand, South Africa. 226 p.

1982. The fishery for and population dynamics of West Coast rock lobster related to the environment in the Lambert's Bay and Port Nolloth areas. Investl. Rep. Sea Fish. Inst. S. Afr. 124: 57 p.

POLLOCK, D. E., C. J. AUGUSTYN, AND P. C. GOOSEN. 1982. The rock lobster *Jasus lalandii* and its environmental biology on the Saldanha–Columbine fishing ground off the Cape West Coast, 1978–1981. Investl. Rep. Sea Fish. Inst. S. Afr. 125: 30 p.

POLLOCK, D. E., AND G. W. BAILEY. 1986. Rock lobster stranding at Elands Bay. S. Afr. Shipp. News Fish. Ind. Rev. 41(3): 31.

POLLOCK, D. E., AND C. J. DE B. BEYERS. 1981. Environment, distribution and growth rates of West Coast rock lobster *Jasus lalandii* (H. Milne Edwards). Trans. R. Soc. S. Afr. 44: 379–400.

RAND, R. W. 1959. The Cape fur seal *Arctocephalus pusillus:* distribution, abundance and feeding habits off the south western coast of the Cape Province. Investl. Rep. Div. Sea Fish. S. Afr. 34: 75 p.

RIMMER, D. W., AND B. F. PHILLIPS. 1979. Diurnal migration and vertical distribution of phyllosoma larvae of the western rock lobster, *Panulirus cygnus* George. Mar. Biol 54: 109–124.

SCHELTEMA, R. S. 1971. The dispersal of the larvae of shoal-water benthic invertebrate species over long distances by ocean currents, p. 7–28. *In* D. J. Crisp [ed.] Fourth European Marine Biology Symposium. Cambridge University Press, Cambridge.

SHANNON, L. V. 1985. The Benguela ecosystem. Part I. Evolution of the Benguela, physical features and processes. Oceanogr. Mar. Biol. Annu. Rev. 23: 105–182.

SHANNON, L. V., G. H. STANDER, AND J. A. CAMPBELL. 1973. Oceanic

circulation deduced from plastic drift cards. Investl. Rep. Sea Fish. Branch S. Afr. 108: 31 p.

SILBERBAUER, B. I. 1971. The biology of the South African rock lobster *Jasus lalandii* (H. Milne Edwards). 1. Development. Invest. Rep. Div. Sea Fish. S. Afr. 92: 70 p.

SIMS, H. W., AND R. M. INGLE. 1966. Caribbean recruitment of Florida's spiny lobster population. Q. J. Fla. Acad. Sci. 29: 207–242.

WITHAM, R. R., R. M. INGLE, AND E. A. JOYCE. 1968. Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. Fla. State Board Conserv. Tech. Ser. 53: 31 p.

# Recruitment of the Puerulus of the Spiny Lobster, *Panulirus marginatus*, in Hawaii[1]

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MacDonald, C. D. 1986. Recruitment of the puerulus of the spiny lobster, *Panulirus marginatus*, in Hawaii. Can. J. Fish. Aquat. Sci. 43: 2118–2125.

Settlement of pueruli of the Hawaiian spiny lobster, *Panulirus marginatus*, was monitored on a weekly to monthly basis during June 1979 – June 1985 at three islands situated across the extent of the Hawaiian Archipelago to define patterns of recruitment over the species' geographic range. Settlement occurred irregularly throughout the year at French Frigate Shoals near the center, but seasonally during reciprocal times of the year at Kure Atoll and Oahu located at opposite ends of the island chain. There were no significant long-term trends in monthly mean catch per collector. Settlement occurred primarily during the new moon and first quarter lunar phases at each island. The seasonal and geographic patterns of recruitment may be determined to a large extent by an island's position relative to the northern and southern boundaries of the North Pacific Central Water type. Seasonal changes in the position of the principal wind systems of the region, the trades and westerlies, also may influence these patterns. Settlement tended to be higher at the center of the archipelago than at either end and higher in the Northwestern Hawaiian Islands than around the main high islands. Regional differences in catch rates in the commercial fishery may be related to regional differences in puerulus recruitment. Settlement overall was low in comparison with spiny lobsters elsewhere.

L'établissement sur le fond des larves puerulus de la langouste d'Hawaï *Panulirus marginatus* a été surveillé entre juin 1979 et juin 1985, selon un rythme hebdomadaire à mensuel, à trois îles situées aux deux bouts et au centre de l'archipel hawaïen, dans le but de définir la structure du recrutement sur l'ensemble de l'aire de répartition de l'espèce. L'établissement était irrégulier toute l'année aux hauts-fonds French Frigate, près du centre, mais présentait un rythme saisonnier à des périodes comparables à l'atoll Kuré et à Oahu, deux points situés aux extrémités opposées de la chaîne insulaire. Aucune tendance notable à long terme n'a été observée dans la moyenne mensuelle des captures par collecteur. À chaque île, l'établissement sur le fond se produisait principalement à la nouvelle lune et pendant le premier quartier. La structure saisonnière et géographique du recrutement peut être définie dans une grande mesure par la position d'une île par rapport aux limites nord et sud du type d'eau du centre du Pacifique nord. Des changements saisonniers de la position des principaux systèmes de vents de la région, les alizés et les vents d'ouest, peuvent aussi modifier cette structure. Le taux d'établissement sur le fond semble être plus élevé au centre de l'archipel qu'à chacune de ses extrémités, et plus élevé dans les îles du nord-ouest qu'autour des principales îles à haut relief. Les différences régionales dans le taux de capture des pêches commerciales peuvent être liées à des différences régionales dans le recrutement des puerulus. Dans l'ensemble, l'établissement sur le fond est faible par rapport à la situation observée ailleurs chez des langoustes.

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The spiny lobster, *Panulirus marginatus* (Quoy and Gaimard 1825), is endemic to the Hawaiian Archipelago (George and Holthius 1965; Brock 1973). The Hawaiian Archipelago consists of the "main" high volcanic islands (Hawaii through Kauai and Niihau) and extends approximately 1500 km to the northwest as a string of low islands, shoals, and atolls, collectively known as the Northwestern Hawaiian Islands (NWHI) (Fig. 1). A commercial fishery for this species has developed recently in the NWHI. Annual landings in that fishery have ranged from 20 to 500 metric tons since 1977 (Skillman et al. 1986).

Consideration of the pelagic larval stages in managing the fishery for *P. marginatus* is important, since there is potential for wide dispersal of larvae. Maximum larval transport distances range between 483 and 2414 km for several species of spiny lobster (Lazarus 1967; Chittleborough and Thomas 1969; Johnson 1974; Phillips et al. 1979). The potential to disperse within the Hawaiian Archipelago increases the likelihood of extensive gene flow and relates to the degree of stock heterogeneity.

Female *P. marginatus* carry fertilized eggs which hatch into phyllosoma larvae after 30–40 d and become planktonic (Morris 1968). The pelagic existence lasts for 6–11 mo, during which phyllosoma larvae are transported by ocean currents (Phillips and Sastry 1980). Phyllosoma larvae of *P. marginatus* pass through 11 stages (Johnson 1968) before metamorphosing to the postlarval form known as the puerulus.

The puerulus is free-swimming and is the form which returns to nearshore benthic habitats before it settles to the bottom.

[1]Sea Grant Publication UNIHI-SEAGRANT-JC-86-08; ORO Contribution No. 22; HIMB Contribution No. 719.

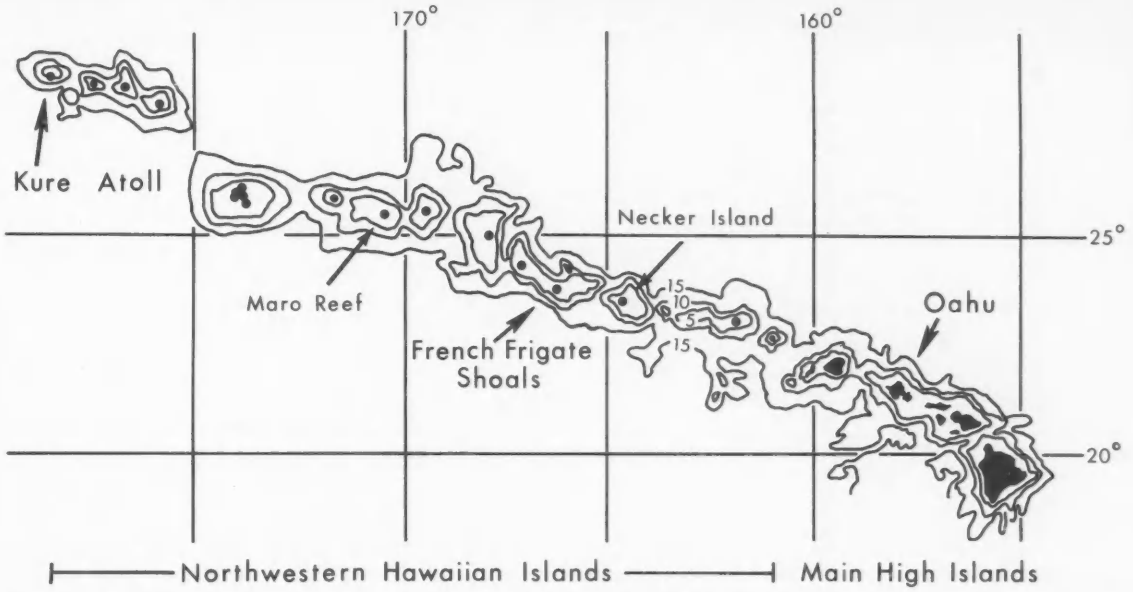


FIG. 1. The Hawaiian Archipelago showing the location of Kure Atoll, French Frigate Shoals, and Oahu where settlement of pueruli of *Panulirus marginatus* was monitored. Other prominent islands and shoals are shaded or designated by solid circles. Bathymetry is in metres (×1000).

TABLE 1. Total, mean, and maximum catch per collector and coefficient of variation (*c*) for *Panulirus marginatus* pueruli and postpueruli during principal periods[a] of settlement over all years combined.

| | Kure Atoll | | | | French Frigate Shoals | | | | Oahu | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Collector | Total | Mean | Max. | *c* | Total | Mean | Max | *c* | Total | Mean | Max | *c* |
| 1 | 26 | 1.13 | 10 | 2.0 | 18 | 0.41 | 3 | 1.8 | 8 | 0.67 | 3 | 2.9 |
| 2 | 22 | 0.88 | 3 | 1.3 | 25 | 0.66 | 4 | 1.6 | 6 | 0.52 | 3 | 3.7 |
| 3 | 28 | 1.32 | 5 | 1.4 | 36 | 0.82 | 5 | 1.3 | 2 | 0.21 | 1 | 4.6 |
| 4 | 27 | 1.46 | 8 | 1.5 | 34 | 0.85 | 4 | 1.2 | 4 | 0.43 | 2 | 4.5 |
| 5 | 22 | 1.64 | 10 | 2.1 | 23 | 0.59 | 3 | 1.4 | 14 | 0.87 | 4 | 2.8 |
| 6 | 14 | 0.56 | 3 | 1.4 | 26 | 0.65 | 3 | 1.3 | 6 | 0.56 | 3 | 4.0 |
| 7 | 36 | 1.44 | 10 | 1.5 | 32 | 0.74 | 5 | 1.6 | 3 | 0.26 | 1 | 3.7 |
| 8 | 36 | 1.33 | 8 | 1.4 | 32 | 0.76 | 3 | 1.2 | 4 | 0.29 | 1 | 3.2 |
| 9 | 37 | 1.76 | 8 | 1.2 | 39 | 1.05 | 6 | 1.5 | 5 | 0.49 | 3 | 4.3 |
| 10 | 54 | 4.54 | 11 | 1.4 | 34 | 0.83 | 6 | 1.6 | 4 | 0.42 | 2 | 4.7 |
| 11 | 61 | 4.78 | 6 | 1.3 | 38 | 1.03 | 8 | 1.6 | | | | |
| 12 | 52 | 2.70 | 11 | 1.1 | 27 | 0.61 | 4 | 1.5 | | | | |
| 13 | 30 | 1.76 | 7 | 1.8 | 24 | 0.53 | 3 | 1.5 | | | | |
| 14 | 93 | 3.88 | 16 | 1.2 | 59 | 1.31 | 7 | 1.2 | | | | |
| 15 | 27 | 1.13 | 4 | 1.2 | 59 | 1.37 | 8 | 1.3 | | | | |
| 16 | 22 | 0.96 | 4 | 1.2 | 33 | 0.83 | 4 | 1.4 | | | | |
| 17 | 17 | 0.61 | 3 | 1.6 | 44 | 1.13 | 8 | 1.6 | | | | |
| 18 | 19 | 0.69 | 3 | 1.4 | 44 | 1.02 | 5 | 1.5 | | | | |
| 19 | 31 | 1.70 | 7 | 2.0 | 60 | 1.46 | 8 | 1.4 | | | | |
| 20 | 44 | 2.29 | 17 | 1.7 | 34 | 0.81 | 6 | 1.6 | | | | |

[a]Kure Atoll (April–October); French Frigate Shoals (January–December); Oahu (September–May).

Upon settling, the puerulus molts into the postpuerulus. The puerulus and postpuerulus of *P. marginatus* are described by Cooke and MacDonald (1981). The long pelagic life typical of phyllosoma larvae of spiny lobsters creates difficulties in studying their recruitment to fishable stocks, but the puerulus and postpuerulus are more amenable in this regard (Witham et al. 1968; Phillips 1972; Chittleborough and Phillips 1975, 1979; Serfling and Ford 1975; Little 1977; Phillips and Hall 1978; Phillips et al. 1978; Booth 1979; Little and Milano 1980).

A major purpose of this study is to provide insights into the environmental process of spiny lobster puerulus recruitment for

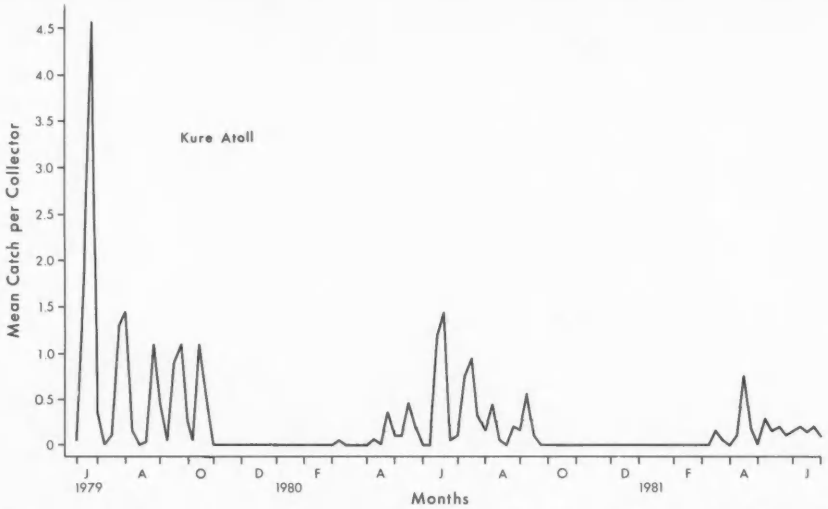


FIG. 2. Weekly mean catch per collector of pueruli and postpueruli of *Panulirus marginatus* at Kure Atoll.

a nonmigratory species restricted to a midoceanic island chain. Related studies have all involved species inhabiting coastal shelves of large land masses (Serfling and Ford 1975; Little 1977; Phillips and Hall 1978; Booth 1979). An investigation of recruitment of the puerulus may help explain regional differences in *P. marginatus* abundance (Uchida and Tagami 1984) and might eventually form the basis for forecasting commercial fishery yields in the NWHI.

## Materials and Methods

Pueruli and postpueruli of *P. marginatus* were caught using floating collectors of the "Witham Habitat" design (Little 1977; Little and Milano 1980). Twenty collectors were moored individually at the surface at permanent stations several hundred metres apart in the lagoon at Kure Atoll (28°25′N, 178°20′W) and within the shelter of the barrier reef at French Frigate Shoals (23°46′N, 166°18′W). Kure Atoll and French Frigate Shoals are state and federal wildlife refuges, respectively. Ten collectors were likewise moored at permanent stations in Kaneohe Bay at Oahu (21°30′N, 158°W) within a restricted area maintained by the U.S. Naval Ocean Systems Center. These collectors were moored about 50 m apart. The location of these islands within the archipelago is indicated in Fig. 1. All collectors were situated amidst patch reef habitats supportive of postpueruli or juveniles as ascertained by diver observations. Water depth at collector stations was generally about 5–10 m.

Collectors were in place at Kure Atoll during June 1979 – October 1983, at Oahu during August 1980 – May 1985, and at French Frigate Shoals during June 1981 – June 1985. Sampling was conducted weekly at Kure Atoll during the first year and monthly thereafter at the time of the full moon. At Oahu and French Frigate Shoals, sampling was done fortnightly at the time of the new and full moon during the first year and monthly thereafter at the time of the full moon. Data collected weekly or fortnightly were pooled on a monthly basis.

Animals were removed from the collectors, frozen, and returned to the laboratory for species identification following the methods of Cooke and MacDonald (1981). The sexes of 360 pueruli were determined electrophoretically (Shaklee 1983) from samples from Kure Atoll during June 1979 – September 1980.

## Results

All pueruli and postpueruli caught in the collectors were *P. marginatus*. This is notable because a second species, *P. penicillatus*, also is common in nearshore waters although generally at low abundance.

Puerulus settlement (capture) was low and variable (Table 1). The number of pueruli that settled differed significantly between collectors at each island (log likelihood ratio test, $P < 0.01$) (Sokal and Rohlf 1969). The test was applied to all samples over the principal periods of settlement. Although variability in the catch by individual collectors was high, the overall pattern of catches for collectors at the same island was similar.

There were no significant long-term trends in monthly mean catch per collector (Spearman rank correlation, $P > 0.05$). For Kure Atoll and French Frigate Shoals, unadjusted monthly mean catches ($n = 48$ and 49, respectively) were used in the analyses. For Oahu, the data for the rank correlation were pooled on a quarterly basis ($n = 19$) to reduce the proportion of tied ranks due to the large number of zero values.

There was no significant difference in the sex ratio of pueruli between collectors at Kure Atoll (log likelihood ratio test, $P < 0.10$). The sex ratio did not differ significantly from 1:1.

Few collectors were lost, and less than 10% of the samplings were missed. The length of immersion did not influence the catch effectiveness of the collectors. After 1 wk, the catch per replacement collector was comparable with the catch of collectors that had been set for much longer.

### Lunar Patterns

Data obtained from weekly sampling at Kure Atoll indicate that puerulus settlement occurs as a series of pulses (Fig. 2). The magnitude of the pulses varies greatly. For example, in 1979, approximately 40% of the year's settlement occurred

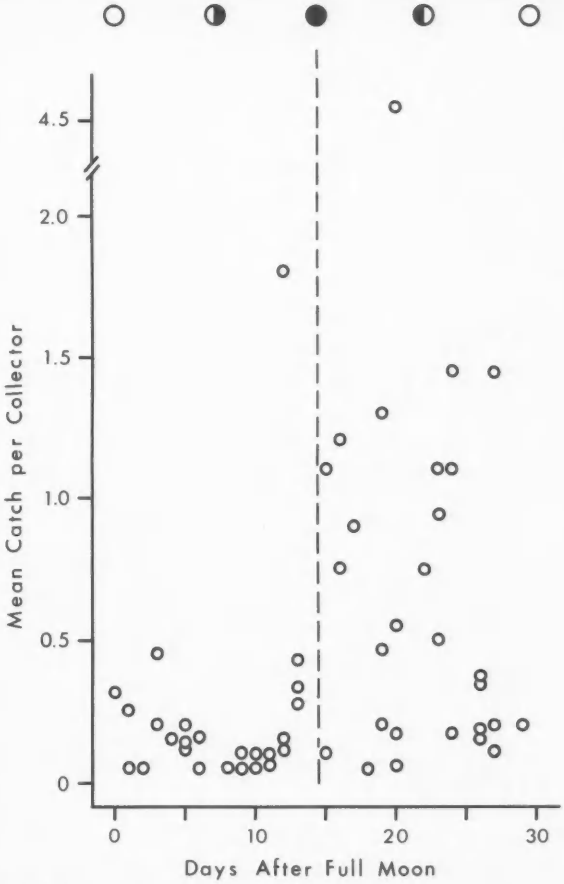


FIG. 3. Lunar pattern of settlement of pueruli of *Panulirus marginatus* at Kure Atoll based on weekly mean catch per collector. Open circles represent full moon, solid circle represents new moon, and half-solid circles represent quarter phases.

within a fortnight in June.

The recruitment pulses at Kure Atoll corresponded to lunar patterns of settlement. From the data, it is evident that significantly more pueruli settled during the new moon and first quarter phases than at other times of the lunar month (Mann–Whitney $U$ test, $P < 0.001$) (Fig. 3). The same timing was also seen in the data from Oahu and French Frigate Shoals.

Individuals settled on the collectors as pueruli, and the degree of development was related to the time of settlement. When collectors were checked around the time of the new moon, all animals were found in the puerulus stage. Newly arrived pueruli were transparent. Pigmentation increased thereafter. When collectors were checked around the time of the full moon, the majority of the pueruli had molted into postpueruli.

### Seasonal and Geographic Patterns

Settlement was seasonal at Kure Atoll (Fig. 4). Significantly more pueruli settled during May–September than during October–April (Mann–Whitney $U$ test, $P < 0.001$). Settlement at Oahu also was seasonal but during the opposite time of the year than at Kure Atoll (Fig. 4). Significantly more pueruli settled during October–April than during May–September (Mann–Whitney $U$ test, $P < 0.05$). Overall, 85% of the settlement at Kure Atoll occurred during May–September; 85% of the settlement at Oahu occurred during October–April. Settlement was not seasonal at French Frigate Shoals, but instead, occurred irregularly throughout the year (Fig. 5).

TABLE 2. Mean catch per collector and standard error (in parentheses) of *Panulirus marginatus* pueruli and postpueruli by locality.

| Year of settlement[a] | Kure Atoll | | French Frigate Shoals | | Oahu | |
|---|---|---|---|---|---|---|
| 1979–80 | 1.39 | (0.55) | — | | — | |
| 1980–81 | 0.72 | (0.26) | — | | 0.10 | (0.06) |
| 1981–82 | 0.68 | (0.31) | 1.01 | (0.21) | 0.23 | (0.13) |
| 1982–83 | 0.57 | (0.17) | 1.01 | (0.08) | 0.13 | (0.07) |
| 1983–84 | — | | 0.71 | (0.13) | 0.03 | (0.02) |
| 1984–85 | — | | 0.76 | (0.20) | 0.01[b] | (0.01) |
| Overall | 0.84 | (0.18) | 0.87 | (0.08) | 0.10 | (0.03) |

[a]Kure Atoll and French Frigate Shoals (June–May); Oahu (August–July).
[b]August–May.

The mean catch per collector is summarized by locality (Table 2). Settlement tended to be higher in the central portion of the archipelago than at either end based on the data for 1981–82 and 1982–83. Settlement was higher in the NWHI than around the main high islands based on the overall means.

## Discussion

High variability in the catches of pueruli by individual collectors in nearby locations is common to other species of spiny lobster (Phillips and Hall 1978; Little and Milano 1980) as is the lunar pattern of settlement (Phillips 1972; Little 1977). Settlement of pueruli of *P. interruptus* in California is an exception in the latter regard because there was no evident lunar relationship (Serfling and Ford 1975). The development of *P. marginatus* pueruli subsequent to settlement is similar to that recorded for other spiny lobsters (Lewis et al. 1952; Phillips 1972; Serfling and Ford 1975; Booth 1979).

The level of settlement of *P. marginatus* was low in comparison with spiny lobsters elsewhere. For example, settlement of *P. argus* along the east coast of Florida (Little 1977; Little and Milano 1980) was at least 100 times greater on the same type of collector as used in Hawaii. Settlement of *P. cygnus* in western Australia also was about 100 times greater, although a different collector was used (Phillips 1972; Phillips and Hall 1978). Some of the difference in the level of settlement between the two species in Hawaii and Australia may be due to the greater sampling efficiency of the Australian collector (Phillips 1972; B. Phillips, CSIRO, Division of Fisheries Research, P.O. Box 21, Cronulla, N.S.W. 2230, Australia, pers. comm.). Using a third type of collector, settlement of *Jasus edwardsii* off the North Island of New Zealand (Booth 1979) was nearly 10 times greater than for *P. marginatus* in Hawaii. The low level of settlement of *P. marginatus* may be associated with two features of the Hawaiian Archipelago.

First, there is no evidence of specific nursery habitat in Hawaii. This may mean that *P. marginatus* pueruli settle broadly at low densities in general habitats. Shallow nearshore algal, seagrass, and mangrove root communities are poorly represented throughout the Hawaiian Archipelago. For other spiny lobsters, such communities typically serve as nursery

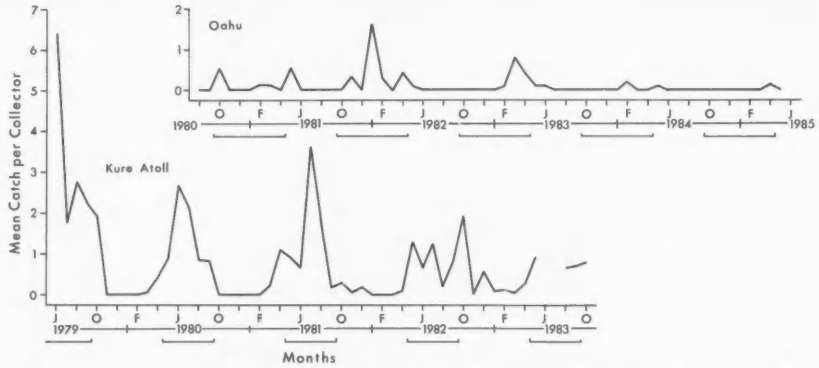


FIG. 4. Monthly mean catch per collector of pueruli and postpueruli of *Panulirus marginatus* at Kure Atoll and Oahu. Brackets indicate the period during which settlement is most likely to occur based on Seckel's (1962) oceanographic climate model.

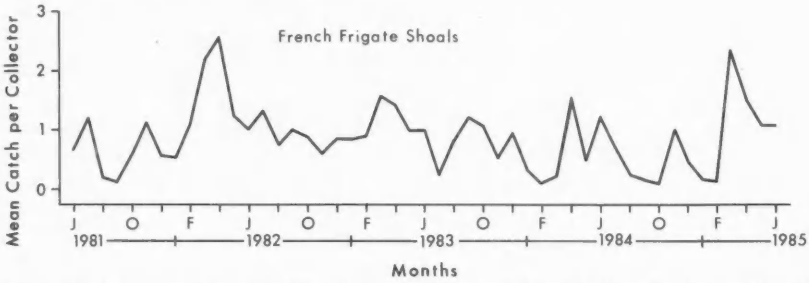


FIG. 5. Monthly mean catch per collector of pueruli and postpueruli of *Panulirus marginatus* at French Frigate Schoals.

habitat for newly settled pueruli and postpueruli and juveniles (Engle 1979; Kanciruk 1980; Marx and Herrnkind 1985). In Hawaii, nursery and adult habitats are indistinguishable (MacDonald and Stimson1980).

Second, the Hawaiian Archipelago is a linear array of small midoceanic islands that are spaced widely apart (Fig. 1). The low level of settlement of *P. marginatus* may reflect a greater loss of larvae to offshore moving eddies or unfavorable currents than occurs routinely along the boundary of large land masses where other species have been studied. As a consequence, the population of *P. marginatus* may be recruitment limited. Recruitment limitation is considered to be one of the most important factors influencing coral reef fish community structure in Hawaii (Walsh 1984). Recruitment of juvenile fishes in Hawaii was 100 times less than on similar reefs on the Great Barrier Reef of Australia.

## Oceanographic Climate and Recruitment

The Hawaiian Archipelago is bathed predominantly by the North Pacific Central Water type (NPCW) (Seckel 1962). The chief distinction between water types and masses is that the former are under the direct influence of physical processes taking place at the sea surface, whereas the latter are not. Boundaries of the NPCW at the northern and southern ends of the archipelago are marked by major frontal zones (Seckel 1962, 1968, 1972; Roden 1981, 1985; VanWoert 1982; Niiler and Reynolds 1984). Movement of the southern boundary northward in summer and southward in winter is a well-established feature (Seckel 1962, 1972; Seckel and Yong 1977). Corresponding seasonal movement of the northern boundary is less well documented, but there is evidence of its occurrence (Seckel 1962; Roden 1970, 1972, 1975, 1980). In effect, it is quite possible that there is a seasonal north–south shift of the entire area of the NPCW within the Hawaiian region.

Larvae of spiny lobsters are known to be useful indicators of water masses in which they originated (Marumo 1957; Johnson and Brinton 1963; McWilliam and Phillips 1983), and frontal systems are believed to be effective zoogeographic barriers in the open ocean (Brandt and Wadley 1981). Assuming that pueruli of *P. marginatus* are associated with the NPCW or some dynamic process(es) associated with it, the seasonal and geographic availability of pueruli may be determined to a large extent by an island's position relative to the NPCW's northern and southern boundaries. Seasonal movement of the southern boundary is associated with seasonal differences in availability of skipjack tuna (*Euthynnus pelamis*) to the Hawaii fishery (Seckel 1972). Since the geographic distribution of *P. marginatus* is limited to the Hawaiian Archipelago, other finer-scale oceanographic conditions such as currents and eddies probably serve to generally retain the phyllosoma larvae within the Hawaiian region (Johnson 1968). A simple model of puerulus settlement based on the seasonal movement of the NPCW appears in MacDonald (1985).

The possible effects of wind-induced surface water movement also bear on the seasonality of puerulus settlement at Kure Atoll and Oahu. The action of surface wind drift is known to be an important larval transport mechanism of spiny lobsters

(Booth 1979; Phillips 1981). Mean sea level atmospheric pressure charts (Namias 1975) show that during the summer, the subtropical HIGH dominates the North Pacific. As this pressure system builds during late winter and spring, the northeast trades strengthen and spread northward. This process is associated with the northward movement of the southern boundary of the NPCW (Seckel 1962). During fall, the trades slacken and the boundary moves southward. Again, mean sea level pressure charts (Namias 1975) show that in fall and winter, the Aleutian LOW dominates the North Pacific north of Hawaii and the northwestern portion of the archipelago comes under the influence of the strong westerly winds.

An experiment with satellite-tracked buoys in the eastern midlatitude North Pacific (McNally 1981) indicates that surface water motion is sensitive to the mean velocities ($>2$ m·s$^{-1}$) of these major wind systems. Subsequent work (McNally et al. 1983) demonstrated that wind-driven flow components associated with seasonal changes in the strength and location of the subtropical HIGH and the Aleutian LOW influence the near-surface circulation of the Hawaiian region. It is possible, therefore, that the wind-induced surface current during fall and winter in the northwestern portion of the archipelago and that during spring and summer in the southeastern portion do not favor puerulus recruitment.

The possible influence of wind-induced surface water movement on larval transport is a functionally different explanation of seasonal patterns of settlement from the one based on the association of larvae with the NPCW. In either case, however, settlement appears to be linked to the environmental processes generally associated with the north–southward shifts of that water type. The intervals designated in Fig. 4 and used in the statistical tests represent the broadest span of time during which puerulus settlement is likely to occur at Kure Atoll and Oahu based on the seasonal pattern of displacement of the NPCW (Seckel 1962). These intervals also correspond to seasonal shifts in the position of the major wind systems of the region (Namias 1975). The timing of reproduction in *P. marginatus* does not determine the timing of puerulus settlement because there is no general consistency between the seasonality of ovigerous females and the seasonality of puerulus recruitment at islands for which such data are available (Morris 1968; C. D. MacDonald, unpubl. data).

### Fishery Management Implications

Differences in catch rates in the commercial fishery at different locations within the archipelago may be related to regional differences in puerulus settlement. The tendency for settlement to be higher in the central portion of the Hawaiian Archipelago than at either end is consistent with the geographic distribution of catch rates in the lobster fishery. The highest catches in the fishery in the NWHI have consistently been made at Necker Island and Maro Reef (Skillman et al. 1986) (Fig. 1). Exploratory fishing throughout the NWHI attests to the highest catch rates, hence lobster densities, occurring at these locations (Uchida and Tagami 1984). Settlement was higher in the NWHI than around the main high islands, which also is consistent with fishery landing statistics. Commercial catches in the NWHI fishery have dwarfed by comparison all recorded commercial catches in the more traditional fishery around the main high islands since 1900 (Morris 1968; Skillman and Ito 1981; Skillman et al. 1986).

An important consideration in managing the fishery is whether there is a single genetically homogenous population throughout the archipelago or whether instead there is a heterogenous assemblage of genetically discrete stocks that differ between islands or groups of islands. In a study of the genetic variation in *P. marginatus*, variability was quite low and no evidence of subpopulation structure or stock heterogeneity was found (Shaklee and Samollow 1980). The hypothesis that pueruli of *P. marginatus* may be associated with the NPCW is consistent with this finding and may represent the underlying mechanism. As the position of the NPCW shifts seasonally in relation to the island chain, there may be sufficient mixing of the larvae while in the plankton that those produced around one island may settle elsewhere in the archipelago. This mechanism would be possible in the case of *P. marginatus* because of the long pelagic larval life. A fishery management plan that treats the spiny lobster resource as a unit stock is consistent with this interpretation.

The annual level of puerulus recruitment to fishery stocks of spiny lobsters can vary greatly between years (Phillips 1981), and the strength of settlement each year may influence future fishery production. In the case of the western Australian spiny lobster *P. cygnus*, for example, the long-term monitoring of the settlement of pueruli has enabled the successful forecasting of commercial fishery yields (Chittleborough and Phillips 1975, 1979; Morgan 1980) and has provided much of the basis for analysis of the stock–recruitment relationship (Morgan et al. 1982). If a similar program of long-term monthly monitoring of the settlement of pueruli of *P. marginatus* is developed in Hawaii for management purposes, several results of this study should be considered.

If use of the "Witham Habitat" design were continued, a greater number of collectors would reduce the variance in estimates of settlement and increase the likelihood of detecting statistical differences between years. For similar reasons, the locality chosen should afford the highest levels of settlement possible; ideally, it should be situated in proximity to the principal commercial fishing grounds for *P. marginatus* in the NWHI. Consequently, any such monitoring program preferably should include an island situated centrally in the Hawaiian Archipelago, such as French Frigate Shoals. Monitoring at islands situated near either end of the archipelago, such as Kure Atoll or Oahu, may be confounded by the interannual variability in boundary transition of the NPCW (Seckel 1962; Seckel and Yong 1977) apart from actual differences in year-class strength of settling pueruli. The choice of geographic location would be especially important if the monitoring program were to be established at only one island.

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## References


BOOTH, J. D. 1979. Settlement of the rock lobster, *Jasus edwardsii* (Decapoda: Palinuridae), at Castlepoint, New Zealand. N.Z.J. Mar. Freshwater Res. 13: 395–406.

BRANDT, S. B., AND B. A. WADLEY. 1981. Thermal fronts as ecotones and zoogeographic barriers in marine and freshwater systems. Proc. Ecol. Soc. Aust. 11:13–26.

BROCK, R. E. 1973. A new distributional record for *Panulirus marginatus* (Quoy and Gaimard, 1825). Crustaceana 25: 111–112.

CHITTLEBOROUGH, R. G., AND B. F. PHILLIPS. 1975. Fluctuations of year-class strength and recruitment in the western rock lobster *Panulirus longipes* (Milne-Edwards). Aust. J. Mar. Freshwater Res. 26: 317–328.

1979. Recruitment to the catchable stock of the western rock lobster *Panulirus longipes cygnus* George. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 139–142.

CHITTLEBOROUGH, R. G., AND L. R. THOMAS. 1969. Larval ecology of the Western Australian marine crayfish, with notes upon other panulirid larvae from the eastern Indian Ocean. Aust. J. Mar. Freshwater Res. 20: 199–223.

COOKE, W. J., AND C. D. MACDONALD. 1981. The puerulus and postpuerulus of the Hawaiian spiny lobster *Panulirus marginatus*. Proc. Biol. Soc. Wash. 94: 1226–1232.

ENGLE, J. M. 1979. Ecology and growth of juvenile California spiny lobster, *Panulirus interruptus* (Randall). Ph.D. thesis, University of Southern California, Los Angeles, CA. 298 p.

GEORGE, R. W., AND L. B. HOLTHIUS. 1965. A revision of the Indo-west Pacific spiny lobsters of the *Panulirus japonicus* group. Zool. Verh. Leid. 72: 1–36.

JOHNSON, M. W. 1968. Palinurid phyllosoma larvae from the Hawaiian Archipelago (Palinuridae). Crustaceana Suppl. II: 59–79.

1974. On the dispersal of lobster larvae into the east Pacific barrier (Decapoda, Palinuridae). Fish. Bull. 72: 639–647.

JOHNSON, M. W., AND E. BRINTON. 1963. Biological species, water-masses and currents, p. 381–414. *In* M. N. Hill [ed.] The sea: ideas and observations on progress in the study of the seas. Vol. 2. Interscience Publishers, New York, NY.

KANCIRUK, P. 1980. Ecology of juvenile and adult Palinuridae (spiny lobsters), p. 59–96. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. II. Academic Press, Inc., New York, NY.

LAZARUS, B. I. 1967. The occurrence of phyllosomata off the cape with particular reference to *Jasus lalandii*. S. Afr. Div. Sea Fish. Invest. Rep. No. 63: 38 p.

LEWIS, J. B., H. B. MOORE, AND W. BABIS. 1952. The postlarval stages of the spiny lobster, *Panulirus argus*. Bull. Mar. Sci. 2: 324–337.

LITTLE, E. J. 1977. Observations on recruitment of postlarval spiny lobsters, *Panulirus argus*, to the south Florida coast. Fla. Mar. Res. Publ. No. 29: 35 p.

LITTLE, E. J., AND G. R. MILANO. 1980. Techniques to monitor recruitment of postlarval spiny lobsters, *Panulirus argus*, to the Florida Keys. Fla. Mar. Res. Publ. No. 37: 16 p.

MACDONALD, C. D. 1985. Oceanographic climate and Hawaiian spiny lobster larval recruitment, p. 127–135. *In* L. Magaard, R. Pujalet, and V. Gaynor [ed.] HOE: The Hawaiian Ocean Experiment. Proceedings of the Hawaiian Winter Workshop. Hawaii Inst. Geophys. Spec. Publ. 1985. University of Hawaii, Honolulu, HI.

MACDONALD, C. D., AND J. S. STIMSON. 1980. Population biology of spiny lobsters in the lagoon at Kure Atoll — preliminary findings and progress to date, p. 161–174. *In* R. W. Grigg and R. T. Pfund [ed.] Proceedings of a symposium on status of resource investigations in the Northwestern Hawaiian Islands. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-80-04. University of Hawaii Sea Grant College Program, Honolulu, HI.

MARUMO, R. 1957. Plankton as the indicator of water masses and ocean currents. Oceanogr. Mag. 9: 55–63.

MARX, J. M., AND W. F. HERRNKIND. 1985. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. Bull. Mar. Sci. 36: 423–431.

MCNALLY, G. J. 1981. Satellite-tracked drift buoy observations of the near-surface flow in the eastern mid-latitude North Pacific. J. Geophys. Res. 86: 8022–8030.

MCNALLY, G. J., W. C. PATZERT, A. D, KIRWAN, JR., AND A. C. VASTANO. 1983. The near-surface circulation of the North Pacific using satellite tracked drifting buoys. J. Geophys. Res. 88: 7507–7518.

MCWILLIAM, P. S., AND B. F. PHILLIPS. 1983. Phyllosoma larvae and other crustacean macrozooplankton associated with eddy J, a warm-core eddy off south-eastern Australia. Aust. J. Mar. Freshwater Res. 34: 653–663.

MORGAN, G. R. 1980. Population dynamics of spiny lobsters, p. 189–217. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. II. Academic Press, Inc., New York, NY.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of western Australia. Fish. Bull. 80: 475–486.

MORRIS, D. E. 1968. Some aspects of the commercial fishery and biology of two species of spiny lobsters, *Panulirus japonicus* (De Siebold) and *Panulirus penicillatus* (Oliver), in Hawaii. M.Sc. thesis, University of Hawaii, Honolulu, HI. 82 p.

NAMIAS, J. 1975. Northern hemisphere seasonal sea level pressure and anomaly charts, 1947–1974. Calif. Coop. Oceanic Fish. Invest. Atlas No. 22: 243 p.

NIILER, P. P., AND R. W. REYNOLDS. 1984. The three-dimensional circulation near the eastern North Pacific subtropical front. J. Phys. Oceanogr. 14: 217–230.

PHILLIPS, B. F. 1972. A semi-quantitative collector of the puerulus larvae of the western rock lobster *Panulirus longipes cygnus* George (Decapoda, Palinuridae). Crustaceana 22: 147–154.

1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

PHILLIPS, B. F., P. A. BROWN, D. W. RIMMER, AND D. D. REID. 1979. Distribution and dispersal of the phyllosoma larvae of the western rock lobster, *Panulirus cygnus*, in the south-eastern Indian Ocean. Aust. J. Mar. Freshwater Res. 30: 773–783.

PHILLIPS, B. F., AND N. G. HALL. 1978. Catches of puerulus larvae on collectors as a measure of natural settlement of the western rock lobster *Panulirus cygnus* George. Aust. CSIRO, Div. Fish. Oceanogr. Rep. No. 98: 18 p.

PHILLIPS, B. F., D. W. RIMMER, AND D. D. REID. 1978. Ecological investigations of the late-stage phyllosoma and puerulus larvae of the western rock lobster, *Panulirus longipes cygnus*. Mar. Biol. 45: 347–357.

PHILLIPS, B. F., AND A. N. SASTRY. 1980. Larval ecology, p. 11–57. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. II. Academic Press, Inc., New York, NY.

RODEN, G. I. 1970. Aspects of the mid-Pacific transition zone. J. Geophys. Res. 75: 1097–1109.

1972. Temperature and salinity fronts at the boundaries of the subarctic–subtropical transition zone in the western Pacific. J. Geophys. Res. 77: 7175–7187.

1975. On North Pacific temperature, salinity, sound velocity and density fronts and their relation to the wind and energy flux fields. J. Phys. Oceanogr. 5: 557–571.

1980. On the subtropical frontal zone north of Hawaii during winter. J. Phys. Oceanogr. 10: 342–362.

1981. Mesoscale thermohaline, sound velocity and baroclinic flow structure of the Pacific subtropical front during the winter of 1980. J. Phys. Oceanogr. 22: 658–675.

1985. Mesoscale thermohaline structure in the vicinity of the Hawaiian islands, p. 139–159. *In* L. Magaard, R. Pujalet, and V. Gaynor [ed.] HOE: The Hawaiian Ocean Experiment. Proceedings of the Hawaiian Winter Workshop. Hawaii Inst. Geophys. Spec. Publ. 1985. University of Hawaii, Honolulu, HI.

SECKEL, G. R. 1962. Atlas of the oceanographic climate of the Hawaiian Islands region. U.S. Fish Wild. Serv. Fish. Bull. 61: 371–427.

1968. A time-sequence oceanographic investigation in the North Pacific trade-wind zone. Trans. Am. Geophys. Union 49: 377–387.

1972. Hawaiian-caught skipjack tuna and their physical environment. Fish. Bull. 70: 763–787.

SECKEL, G. R., AND M. Y. Y. YONG. 1977. Koko Head, Oahu, sea-surface temperatures and salinities, 1956–73, and Christmas Island sea-surface temperatures, 1954–73. Fish. Bull. 75: 767–787.

SERFLING, S. A., AND R. F. FORD. 1975. Ecological studies of the puerulus larval stage of the California spiny lobster *Panulirus interruptus* (Randall). Fish. Bull. 73: 360–377.

SHAKLEE, J. B. 1983. Mannosephosphate isomerase in the Hawaiian spiny lobster *Panulirus marginatus*: a polymorphic, sex-linked locus useful in investigating embryonic and larval sex ratios. Mar. Biol. 73: 193–201.

SHAKLEE, J. B., AND P. B. SAMOLLOW. 1980. Genetic aspects of population structure of four species in the Northwestern Hawaiian Islands,

p. 264–277. *In* R. W. Grigg and R. T. Pfund [ed.] Proceedings of the symposium on status of resource investigations in the Northwestern Hawaiian Islands. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-80-04. University of Hawaii Sea Grant College Program, Honolulu, HI.

SKILLMAN, R. A., AND B. M. ITO. 1981. The present status of the spiny lobster fishery in Hawaiian waters. Southwest Fish. Cent. Natl. Mar. Fish. Serv. NOAA Admin. Rep. H-81-7: 4 p.

SKILLMAN, R. A., P. A. MILONE, AND H. E. WITHAM. 1986. Annual report of the 1985 Western Pacific lobster fishery. Southwest Fish. Cent. Natl. Mar. Fish. Serv. NOAA Admin. Rep. H-86-6: 43 p.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Company, San Francisco, CA.

UCHIDA, R. N., AND D. T. TAGAMI. 1984. Biology, distribution, population structure, and pre-exploitation abundance of spiny lobster, *Panulirus marginatus* (Quoy and Gaimard 1825), in the Northwestern Hawaiian Islands, p. 157–198. *In* R. W. Grigg and K. Y. Tanoue [ed.] Proceedings of the second symposium on resource investigations in the Northwestern Hawaiian Islands, Vol. I. Sea Grant Misc. Rep. UNIHI-SEAGRANT-MR-84-01. University of Hawaii Sea Grant College Program, Honolulu, HI.

VANWOERT, M. 1982. The subtropical front: satellite observations during FRONTS 80. J. Geophys. Res. 87: 9523–9536.

WALSH, W. J. III. 1984. Aspects of nocturnal shelter, habitat space, and juvenile recruitment in Hawaiian coral reef fishes. Ph.D. thesis, University of Hawaii, Honolulu, HI. 475 p.

WITHAM, R., R. M. INGLE, AND E. A. JOYCE. 1968. Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. Fla. Board Conserv. Mar. Res. Lab. Tech. Ser. No. 53: 31 p.

# Prediction of Commercial Catches of the Western Rock Lobster *Panulirus cygnus*

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Phillips, B. F. 1986. Prediction of commercial catches of the western rock lobster *Panulirus cygnus*. Can. J. Fish. Aquat. Sci. 43: 2126–2130.

Predictions of the size of the Western Australian commercial catch of the western rock lobster *Panulirus cygnus* have been successfully made 4 yr ahead. The predictive system, which has operated for 9 yr has been recognized by industry and government as an important tool in the management of Australia's most valuable single-species fishery. The accurate prediction depends on demonstrated relationships between the number of rock lobsters at the puerulus stage of their development (the last stage of its pelagic existence) and the level of recruitment to the fishery, and the total catch of the fishery, 4 yr after settlement. Since 1980, predictions of the catches have been based on settlement data from a single site, Seven Mile Beach, which is near the centre of the distribution of the species. The catches of the fishery from 1961–62 to 1983–84 ranged from $6.8 \times 10^6$ kg in 1973–74 to $12.4 \times 10^6$ kg in 1982–83. Based on a regression of total catches from 1969 to 1979 on puerulus settlement, and allowing for a trend of increasing catch with time, the total catch is predicted to fall to about $7.72 \times 10^6$ kg in 1986–87 because of the low level of puerulus settlement in 1982–83. However, increased settlement in 1983–84 and the highest settlement ever recorded in 1984–85 indicate that catches should increase for the 1987–88 fishing season. Similar relationships between life history stages can be discerned for other crustacean species, provided accurate, long-term data are available.

Le volume des prises commerciales de la langouste *Panulirus cygnus* dans l'ouest de l'Australie a pu être prédit avec succès 4 ans à l'avance. Le système de prédiction, qui fonctionne depuis 9 ans, est considéré par l'industrie et par le gouvernement comme un outil important dans la gestion de la plus précieuse des pêches monospécifiques de l'Australie. Pour être exacte, la prédiction doit se fonder sur les relations qui ont été démontrées entre le nombre de langoustes au stade puerulus (dernier stade de la phase pélagique) et le recrutement pour la pêche, et les captures totales, quatre ans après l'établissement sur le fond. Depuis 1980, les prédictions des prises se fondent sur les données concernant l'établissement sur le fond provenant d'un seul site, Seven Mile Beach, qui se trouve près du centre de l'aire de répartition de l'espèce. Le volume des prises entre 1961–62 et 1983–84 allait de $6{,}8 \times 10^6$ kg en 1973–74 à $12{,}4 \times 10^6$ kg en 1982–83. En calculant l'établissement sur le fond des puerulus par régression à partir des prises totales entre 1969 et 1979, et en tenant compte d'une tendance à l'augmentation des prises avec le temps, on prévoit que le total des prises devrait se situer aux alentours de $7{,}72 \times 10^6$ kg en 1986–87 à cause du faible taux d'établissement des puerulus en 1982–83. Toutefois, l'augmentation du taux d'établissement en 1983–84 et le record observé en 1984–85 indiquent que les prises devraient augmenter à la saison de pêche 1987–88. Il est possible de repérer des relations semblables entre les stades biologiques chez d'autres espèces de crustacés à condition de disposer de données exactes et recueillies sur une longue période.

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The western rock lobster *Panulirus cygnus* George, Australia's most valuable single-species fishery, is found on the west coast of Australia from approximately North West Cape to Augusta (Sheard 1962) (Fig. 1) and was worth over $A130.1 million in 1984–85. Most of the catch is taken between South Passage (Shark Bay) and Augusta and at the Abrolhos Islands (Bowen 1980).

The commercial fishery operates on immature and mature rock lobsters with substantial fishing effort directed at the emigrating juveniles. These juveniles are pale in colour and are known as "whites." Those that have attained legal size are the recruits to the fishery. The coastal fishery operates from 15 November to 30 June, while the fishery at the Abrolhos Islands operates from 15 March to 30 June.

The complex life cycle of the rock lobster includes an oceanic phase of 9–11 mo (Phillips 1981). The nektonic stage (the last pelagic stage) completes the oceanic cycle by swimming to the coast and settling in the shallow inshore limestone reef areas. The peak settlement of puerulus occurs between September and January, following hatching in the previous December to February period (Phillips et al. 1979). Based on the time of hatching of the phyllosoma larvae, Morgan et al. (1982) adopted 1 January, the midpoint of the hatching period, as an arbitrary "birthday," so that the age of newly settled puerulus is 0+ to 1+ yr, and they are all taken as 1 yr old on 1 January.

The settled puerulus moults into a small juvenile lobster about 3 cm long that is morphologically similar to the adult. These juvenile lobsters remain in the shallow coastal reefs for up to 6 yr (Chittleborough 1970; Chittleborough and Phillips 1975). At 4–6 yr of age the juveniles migrate offshore into depths of 30–200 m (Morgan et al. 1982) during November to January.

Successful prediction of commercial catches depends on the availability of long-term, accurate data and demonstrated relationships between life history stages. However, despite their importance, quantitative data on stock–recruitment relation-

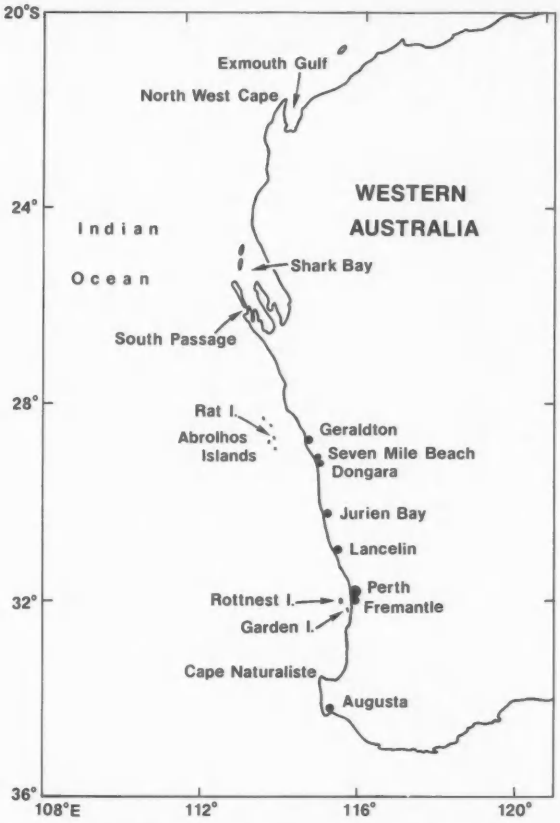


FIG. 1. Sites mentioned in the text. Most of the catch of *Panulirus cygnus* is taken between South Passage (Shark Bay) and Augusta, and at the Abrolhos Islands.

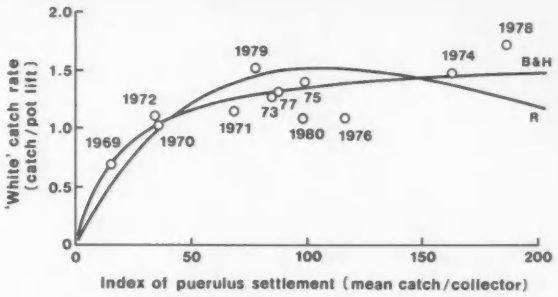


FIG. 2. Indices of annual puerulus settlement at Seven Mile Beach for 1969–80 and catch rates of *Panulirus cygnus* "whites" 4 yr later. Ricker (1958) (R) and Beverton and Holt (1957) (B & H) fitted curves. The year shown is the year of puerulus settlement.

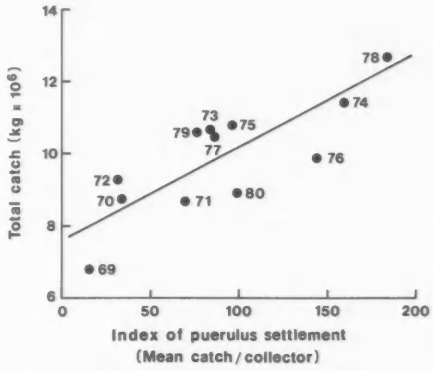


FIG. 3. Indices of annual puerulus settlement at Seven Mile Beach for 1969–80 and the total commercial catch of *Panulirus cygnus* 4 yr later. The fitted regression is $Y = 7.50 + 0.0264X$. The year shown is the year of puerulus settlement.

ships for crustaceans were until recently virtually nonexistent (Hancock 1973). However, Morgan et al. (1982) demonstrated relationships between several stages in the life cycle of the western rock lobster *P. cygnus* in Western Australia.

As reported by Hancock (1981) and Morgan et al. (1982), the close relationship between the level of puerulus settlement and subsequent abundance of recruits to the fishery means that the level of puerulus settlement can be used as an indicator of the likely level of the catches of the future fishery.

The purpose of this paper is to examine the usefulness and application of the prediction system for the catches of the western rock lobster fishery and to describe recent developments, including the use of settlement data from a single site to make the predictions.

## Methods

### Index of Annual Settlement

Phillips (1972) showed that the last oceanic stage, the puerulus, of *P. cygnus* could be captured with collectors composed of artificial seaweed moored at the surface within the protection of the coastal reefs. Subsequently, Phillips and Hall (1978) showed that sizes of catches from these collectors provide a measure or index of the relative strength of puerulus settlement.

Collectors used in this study were described by Phillips (1972). They were checked monthly after each new moon period when most puerulus settle. The lobsters were removed from the collectors either as puerulus or as small, newly moulted post-juveniles.

The index of annual settlement used by Morgan et al. (1982) was the mean level of settlement of the puerulus stage (catch per collector per year) on collectors at four sites: Garden Island, Jurien Bay, Seven Mile Beach, and Rat Island (Abrolhos Islands). In 1980, collection from Garden Island and Rat Island was discontinued. The puerulus data from Rat Island and Jurien Bay were shown to have a high correlation with the data from Seven Mile Beach (Morgan et al. 1982), and only data from Seven Mile Beach are used in this paper. These consist of data from October 1967 to May 1985 on the catches of six collectors. The index of annual settlement is calculated as the mean catch per collector per season.

### Abundance of Recruits to the Coastal Fishery

The abundance was calculated from the catch rate (catch per pot lift) of the commercial fishery during November and December, when between 50 and 66% of the commercial catch consists of "white" rock lobsters recruited from the coastal reefs (Chittleborough and Phillips 1975).

Information on catch and fishing effort for November and

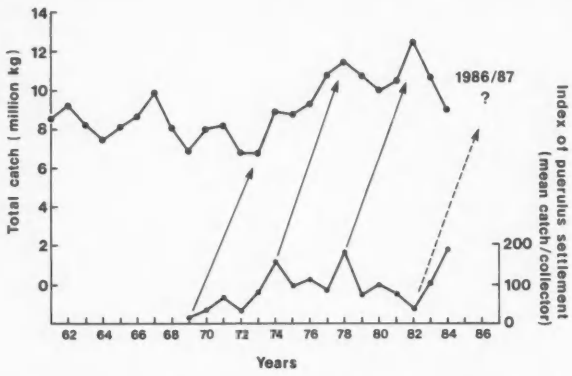


FIG. 4. Indices of annual puerulus settlement at Seven Mile Beach for 1969–84 and the total commercial catch of *Panulirus cygnus* from 1961–62 to 1984–85.

December each year was taken from the fishermen's Australian Bureau of Statistics monthly returns, which are completed by all fishermen as a condition of their fishing licences.

### Methods of Prediction

Two methods to predict the catch were used.

*Method 1*: A regression of the total catch on the puerulus settlement data for 1969–80. This regression is linear (no significant quadratic or higher order terms) and accounts for 74% of the total variance (25.09) of the total catch data.

*Method 2*: The first method does not take into account the time trends in the catch and the puerulus settlement data. Both the catch and puerulus settlement data show increases and decreases with time (see Fig. 4). To do this, three quadratic regressions of the total catch and puerulus were fitted. The first regression is the total catch data from 1969–80 and accounted for 77% of the total variance. The second regression was of the puerulus settlement data from 1969–82 and accounted for 57% of the variance. The residuals from the regression of the total catch data were then regressed against those for the puerulus settlement data. This regression is quadratic and accounts for a further 70% of the remaining variance (4.03) of the total catch data. All regressions are highly significant.

## Results and Discussion

### The Prediction System

Following the low settlement of puerulus on the collectors in 1969–70 and low densities of early juveniles eventuating from this settlement, it was predicted in 1971 that low catch levels would be likely in 1972–73 and even lower ones likely in 1973–74 season (Hancock 1971). This prediction was borne out by the poor catches of these two years (Anonymous 1974), the "white" season of 1973–74 being the poorest on record.

Since 1980, the data from Seven Mile Beach alone have been used to predict both the annual "white" fishery 4 yr later and to predict the total catch of the fishery. The relation between the level of puerulus settlement and the level of recruits to the fishery 4 yr later calculated by Morgan et al. (1982) was obtained by fitting the Ricker (1958) stock–recruitment relationship. The levels of puerulus settlement at Seven Mile Beach, and of recruits to the fishery 4 yr later, are shown in Fig. 2. Data obtained since the paper by Morgan et al. (1982) have increased the scatter of the data, but good fits of the models of both Ricker (1958) and Beverton and Holt (1957) were obtained. The fit of the Ricker model was obtained by linear regression on log-transformed versions of the data. For both models the variance accounted for on the transformed scale was 86% and this is shown by the close fit of the data to the fitted curves. However, it is clear that the closeness of its relationship partly depends on the very low (1969) and high (1978) data points.

The commercial catch of any year is composed of a number of year-classes, but because the "white" fishery catch is about 40% of the total, it strongly influences the total catch. The levels of puerulus settlement at Seven Mile Beach plotted against the total commercial catch of the fishery 4 yr later are shown in Fig. 3. The strong linear relationship is confirmed by a linear regression of the data ($r = 0.862$, $p < 0.001$). However, a clear time trend is apparent in the catch data with a progressive increase in the catch that levelled off in the final years (Fig. 4). Figure 4 is the typical form of the data as presented to fishermen and others interested in future catches in the fishery.

### The Future Fishery

The catches arising from the settlements of the years 1969–78 varied between $6.8 \times 10^6$ and $12.4 \times 10^6$ kg. However, factors other than the settlement level are involved in variations of annual catch. The increase in fishing effort from $9.8 \times 10^6$ pot lifts in 1973–74 to an unprecedented $11.2 \times 10^6$ pot lifts in 1981–82 (R. S. Brown, Fisheries Department, Western Australia, pers. comm.) appears to be a factor contributing to the trend in increasing total catch with time. The level of the breeding stock is related initially to the level of recruitment at the puerulus stage and then to the fishing pressure on the adults after they enter the fishery (Morgan et al. 1982). The effect of strong fishing pressure, combined with a low level of puerulus settlement, may further reduce the breeding stock size, possibly below the critical level to maintain recruitment to the fishery at the current levels.

The levels of puerulus settlement at Seven Mile Beach and observed and predicted levels of catches 4 yr later are given in Table 1. The predictions using method 1 are extremely conservative, and most levels of settlement will predict catches close to the mean level of catch. The catch has varied by approximately two times, while settlement has varied by approximately 18 times, but method 1 does not take into account either decreasing or increasing trends in the level of settlement or catch. Method 2 allows for these time trends and is more accurate. Using a regression of the levels of puerulus settlement/total catch data from 1969 to 1978, and allowing for the trend of increasing catch with time based on the level of puerulus settlement in 1979 (method 2), it was predicted that the total catch in 1983–84 would be $10.04 \times 10^6$ kg. The catch was $10.59 \times 10^6$ kg. Based on the data to 1980 and the level of puerulus settlement in 1982, it is predicted that the total western rock lobster catch in the 1986–87 season should be in the region of $7.72 \times 10^6$ kg. This prediction assumes that both the level of effort and the environmental conditions will be similar to those experienced over the last decade. Because the level of puerulus settlement in 1983–84 (Fig. 4) was substantially higher than for several past years (and 1984–85 the highest ever recorded), the catches can be expected to increase

TABLE 1. Levels of settlement at Seven Mile Beach and observed and predicted catches 4 yr later (— = note yet available).

| Year of settlement | Index of puerulus settlement (mean catch per collector) | Observed total catch ($10^6$ kg) | Predicted method 1 total catch (±SE) ($10^6$ kg) | Predicted method 2 total catch (±SE) ($10^6$ kg) |
|---|---|---|---|---|
| 1969 | 15.2 | 6.77 | 7.90 (0.92) | 6.65 (0.93) |
| 1970 | 35.0 | 8.26 | 8.42 (0.89) | 7.63 (0.90) |
| 1971 | 67.3 | 8.72 | 9.28 (0.86) | 8.64 (0.88) |
| 1972 | 33.7 | 9.31 | 8.39 (0.86) | 9.56 (0.87) |
| 1973 | 83.2 | 10.05 | 9.70 (0.89) | 9.86 (0.86) |
| 1974 | 159.8 | 11.39 | 11.72 (0.86) | 11.54 (0.85) |
| 1975 | 97.3 | 10.71 | 10.07 (0.94) | 10.57 (0.85) |
| 1976 | 114.3 | 9.93 | 10.52 (0.86) | 10.68 (0.86) |
| 1977 | 86.0 | 10.55 | 9.78 (0.87) | 10.71 (0.87) |
| 1978 | 182.8 | 12.42 | 12.33 (0.86) | 12.30 (0.88) |
| 1979 | 76.2 | 10.59 | 9.51 (0.99) | 10.04 (0.90) |
| 1980 | 98.8 | 8.97 | 10.11 (0.86) | 9.51 (0.92) |
| 1981 | 83.0 | — | 9.69 (0.86) | 8.79 (0.94) |
| 1982 | 40.3 | — | 8.56 (0.89) | 7.72 (0.95) |

again after the 1986–87 season.

The predictions are updated annually as additional data on the catches and the levels of puerulus settlement become available. However, the model relating puerulus settlement to recruitment used in this paper is likely to change as additional data clarifying the nature of the interaction between the level of puerulus settlement and catch become available. For example, this relationship may be the result of a particular environmental pattern and this may change over time.

The use of data from Seven Mile Beach as a sole measure of puerulus settlement involves assumptions regarding the distribution of puerulus settlement along the coast of Western Australia. Studies were initiated in 1984 to examine spatial and temporal variability of settlement over the range of the fishery at seven sites from South Passage Shark Bay to Augusta (Fig. 1) to add to our understanding of the recruitment process. Using remote sensing techniques, we may be able to deduce the factors causing variations in seasonal patterns of settlement at different sites and also the causes of variations in the levels of annual puerulus settlement.

## Recognition of the Prediction System

The accuracy of the predictions of the annual catch, particularly of the "white" fishery, has proved useful for the management of the fishery (Hancock 1981; Anonymous 1982, 1983a; Parker 1983) and organisations involved with the fishing industry, e.g. fishermen, fishing companies, processors, banks (see France 1983). Many fishermen seek information on catch predictions when they are contemplating new developments, e.g. the purchase of a new vessel or additional pot licences, and banks use information on the predictions from the puerulus settlement data in their consideration of lending policies to the fishing industry.

The most important use of the predictive system has been that it has allowed those managing the fishery to anticipate years of reduced catches and to explain that the falling catches are caused by a natural fluctuation in abundance, rather than by overfishing of the resource. Discussions with those responsible for management of the fishery (B. K. Bowen, Fisheries Department, Western Australia, pers. comm.) have revealed that the accuracy of the catch prediction in any year is of less importance than a prediction of trends in catch which will occur. The actual level of catch will depend on many factors including fishing effort, technological developments, and the weather. However, a knowledge that availability of the stock will be decreased or increased will allow those managing the fishery to take appropriate action.

Data on puerulus settlement levels are routinely considered in estimate considerations of likely future fishing success given to fishermen and the State Government Minister responsible for the fishery by the Industry Advisory Committee (Anonymous 1984).

An important feature of the recent puerulus settlement data was the reduced levels of settlement since the peak in 1978–79. The level of settlement in 1982–83 approached the low level recorded in 1969–70. This was of major concern to those managing the fishery. The relationship between the index of the spawning stock and resultant level of puerulus settlement in *P. cygnus* (Morgan et al. 1982; Fig. 2) provided a clear warning that a recruitment failure might occur if effort were to increase still further. The increased level of settlement in 1983–84 and 1984–85 has reduced the likelihood that the breeding stock has been overfished, allaying their own and the fears of the fishermen.

Setting quotas on catches is an option that has been considered by those managing the *P. cygnus* fishery (Anonymous 1984), and obviously the predictive system would be useful for calculating such quotas if they were introduced.

## Stock–Recruitment Relationships in Other Crustaceans

No relationships linking settlement at the end of the pelagic cycle to the abundance of adults (or between any other stages in the life cycle) have yet been described for any other species of rock (spiny) lobster or other lobsters. However, the fact that stock–recruitment relationships have not been demonstrated in any lobster species is probably because suitable data have not been collected.

Stock–recruitment relationships recently have been described in two other crustacean species. (1) McKelvey et al. (1980) examined stock and recruitment in the Northern Cali-

fornia Dungeness crab *Cancer magister* with the use of a multistage recruitment model. The *C. magister* fishery is similar to that of *P. cygnus* in that it is heavily exploited and only a few age-classes are represented in the landings. The crab landings have exhibited a regular cycling pattern since the early 1940s, but of increasing amplitude swings as the fishery expanded, suggesting the possibility of an eventual crash. The overall conclusion from their study was that stock–recruitment relationships exist and that recruitment is determined mainly in either the egg or larval stages. (2) Shrimp populations have traditionally been regarded as unaffected by fishing effort (Garcia and Le Reste 1981). Garcia (1983) concluded that published stock and recruitment relationships on shrimp are likely to be statistical artefacts or biological misinterpretations. However, a study of the brown tiger prawn (shrimp) *Penaeus esculentus* Haswell in Exmouth Gulf in Western Australia (Penn 1984) has indicated that both spawning stock and recruitment were reducing and fishing effort was increasing over a period of 15 yr. Environmental factors may be responsible, but the inference that fishing effort was reducing spawning stock to levels at which subsequent recruitment was affected was sufficiently strong to cause fisheries managers to close the fishery. Monitoring of the breeding stocks since the closure has indicated that, within only 2 yr, the closure may have effectively improved recruitment of *P. esculentus* in 1984 (Anonymous 1983b).

## Conclusions

The general problem related to stock–recruitment data has been accurately described by McKelvey et al. (1980): "The fishery biologist may likely never collect enough data to allow confident statistical descriptions of such complex processes." However, where long-term accurate data are available, stock–recruitment relationships can be clearly shown.

Gulland (1973) concluded that from the data available to him that the study of stock and recruitment was not generally useful to management decisions. This was principally because data are both time-consuming and costly to collect, and precise analysis is difficult, and there is usually a lack of understanding of the mechanisms producing the observed variations in recruitment.

The western rock lobster fishery was worth more than $A130.1 million in landed catch to the fisherman in 1984–85. Hancock (1981) estimated the cost to the State Management Authority of administration, inspection, and research at about 2.5% of the gross landed value of the catch. Of this 2.1% (about $A683 000 in 1984) was for research. With the prediction system which is in operation for *P. cygnus*, the fishermen, processors, and those managing the fishery can anticipate changes in levels of the catch and take appropriate action, 4 yr in advance. The potential for saving millions of dollars far exceeds the cost of research.

Although the collection of data for analysis of stock–recruitment relationships is time-consuming and expensive, the advantages as demonstrated by the western rock lobster example far outweigh the costs. Worth noting is the magnitude of changes in the levels of settlement that have been recorded in this study. The duration of many research programs is 3–5 yr. This would be insufficient to predict variations in settlement of the magnitude that occurs in *P. cygnus*. The collection of long-term data is essential.

## Acknowledgements

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## References

ANONYMOUS. 1974. 1973–74 rock lobster season poorest for five years. Aust. Fish. 33(9): 2.

1982. The 1981–82 rock lobster season and predictions for 1982–83. FINS 15(1): 10–12.

1983a. Rock Lobster Industry Advisory Committee meetings. FINS 16(2): 11–16.

1983b. Exmouth Gulf prawn fishery. FINS 16(3): 23.

1984. Report of the Rock Lobster Advisory Committee. FINS 17(1): 7–11.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. (Lond.) Ser. 2(19): 1–533.

BOWEN, B. K. 1980. Spiny lobster fishery management, p. 243–264. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. II. Academic Press, New York, NY. 390 p.

CHITTLEBOROUGH, R. G. 1970. Studies on recruitment in the Western Australian rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. Aust. J. Mar. Freshwater Res. 21: 131–148.

CHITTLEBOROUGH, R. G., AND B. F. PHILLIPS. 1975. Fluctuations of year-class strength and recruitment in the western rock lobster *Panulirus longipes* (Milne-Edwards). Aust. J. Mar. Freshwater Res. 26: 317–328.

FRANCE, M. 1983. Industry's view of the shellfish markets. Aust. Fish. Feb. 42(2): 16–17, 28.

GARCIA, S. 1983. The stock–recruitment relationship in shrimps: reality or artefacts and misinterpretations? Oceanogr. Trop. 18(1): 25–48

GARCIA, S., AND I. LE RESTE. 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish. Tech. Pap. No. 203: 215. (Issued also in French)

GULLAND, J. A. 1973. Can a study of stock and recruitment aid management decisions? Rapp. R.-V. Reun. Cons. Perm. Int. Explor. Mer 164: 368–372.

HANCOCK, D. A. 1971. Rock lobsters: what of the future? Fish. Ind. News Serv. 4: 47.

1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 164: 113–131.

1981. Research for management of the rock lobster fishery of Western Australia. Proc. Gulf. Caribb. Fish. Inst. 33: 207–229.

MCKELVEY, R., D. HANKIN, K. YANOSKO, AND C. SNYGG. 1980. Stable cycles in multistage recruitment models: an application to the Northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37: 2323–2345.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia. Fish. Bull. 80(3): 475–486.

PARKER, D. 1983. Record W.A. rock lobster season. Aust. Fish. Sept.: 2–3.

PENN, J. W. 1984. The behaviour and catchability of some commercially exploited penaeids and their relationship to stock and recruitment, p. 173–186. *In* J. A. Gulland and B. J. Rothschild [ed.] Penaid shrimps — Their biology and management. Fishing News Books Ltd., Surrey, England.

PHILLIPS, B. F. 1972. A semi-quantitative collector of the puerulus larvae of the western rock lobster *Panulirus longipes cygnus* George (Decapoda: Palinuridae). Crustacean 22: 147–154.

1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Annu. Rev. 19: 11–39.

PHILLIPS, B. F., P. A. BROWN, D. W. RIMMER, AND D. D. REID. 1979. Distribution and dispersal of the phyllosoma larvae of the western rock lobster, *Panulirus cygnus*, in the south-eastern Indian Ocean. Aust. J. Mar. Freshwater Res. 30: 773–783.

PHILLIPS, B. F., AND N. G. HALL. 1978. Catches of puerulus larvae on collectors as a measure of natural settlement of the western rock lobster *Panulirus cygnus* George. CSIRO Aust. Div. Fish. Oceanogr. Rep. 89: 1–18.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish. Res. Board Can. 119: 300 p.

SHEARD, K. 1962. The Western Australian crayfishery 1944–1961. Paterson Brokensha, Perth. 107 p.

# Relationship Between Indices of Juvenile Abundance and Recruitment in the Western Rock Lobster (*Panulirus cygnus*) Fishery

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Caputi, N., and R. S. Brown. 1986. Relationship between indices of juvenile abundance and recruitment in the western rock lobster (*Panulirus cygnus*) fishery. Can. J. Fish. Aquat. Sci. 43: 2131–2139.

Indices of abundance of 3- and 4-yr-old juvenile western rock lobsters (*Panulirus cygnus*) were used to determine the status of the stocks between the puerulus stage and subsequent recruitment to the fishery. These indices were based on logarithmically transformed catch rate data of undersize lobsters obtained from a monitoring program which commenced in 1971–72. The juvenile indices were determined from regression coefficients associated with the factor "year", adjusted for other factors, e.g. location, month, depth, soak time, which affect juvenile catch rates. A revised index of recruitment was based on logarithmically transformed catch rates, in depths up to 18 m. A 7-d moving average was used to smooth out daily fluctuations to enable the "best" 60-d catch rate over the period of recruitment to the fishery (November–January) to be determined so that differences in the time of recruitment may be taken into account in quantifying the level of recruitment. This index is compared with a previous recruitment index based on total catch divided by total effort during November–December. The relationships between the abundance indices of 3- and 4-yr-old male juveniles and the recruitment index resulted in correlations of 0.95 and 0.93, respectively, from the log–log analyses of 11 year-classes with a multiple correlation of 0.97 when the 3- and 4-yr-old indices were used in a multiple regression. These indices provide an independent method to support or modify the prediction of recruitment based on an index of abundance of settling puerulus (aged 9–11 mo) obtained 4 yr before they recruit into the fishery.

Les indices de l'abondance des juvéniles de langoustes (*Panulirus cygnus*) âgés de 3 et 4 ans ont servi à déterminer l'état des stocks entre le stade puerulus et le recrutement pour la pêche. Ces indices ont été établis à partir de données, mises sous forme logarithmique, sur les prises de langoustes de taille inférieure à la taille légale, données obtenues grâce à un programme de surveillance lancé en 1971–72. Les indices ont été calculés à l'aide de coefficients de régression associés au facteur « année », rajustés en fonction d'autres facteurs, par exemple le lieu, le mois, la profondeur, le temps de mouillage, qui affectent les taux de capture des juvéniles. Un indice du recrutement révisé a été établi par transformation logarithmique des taux de capture, à des profondeurs allant jusqu'à 18 m. Une moyenne mobile sur sept j a servi à effacer les fluctuations quotidiennes de façon à permettre de déterminer le « meilleur » taux de capture sur 60 j pendant la période de recrutement pour la pêche (novembre–janvier), ce qui permet de tenir compte des différences dans le moment du recrutement pour calculer le taux de recrutement. Cet indice est comparé à un indice antérieur fondé sur le total des captures divisé par l'effort total en novembre et décembre. Les relations entre les indices de l'abondance des juvéniles mâles âgés de 3 et 4 ans et l'indice du recrutement ont donné des corrélations de 0,95 et 0,93 respectivement, après analyse bilogarithmique de 11 classes annuelles, avec corrélation multiple de 0,97 lorsque les indices des jeunes âgés de 3 et 4 ans étaient utilisés en régression multiple. Ces indices constituent une méthode indépendante permettant d'étayer ou de modifier la prédiction du recrutement fondée sur un indice de l'abondance des puerulus s'établissant sur le fond (9 à 11 mo), indices obtenus 4 ans avant leur recrutement pour la pêche.

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The western rock lobster, *Panulirus cygnus* George, supports one of the world's largest rock lobster fisheries. The average annual catch in the 10 yr to the 1983–84 season was over 10 000 tonnes (t). The catch for the 1983–84 season of 10 700 t provided an income of over $A120 million for the 770 fishing boats. Since the development phase of this fishery, the catches have remained relatively stable, ranging from 6800 t in the 1973–74 season to 12 400 t in the 1982–83 season. This stability has been due partly to strict control through management measures which have been implemented over the years (Bowen 1980; Morgan 1980; Hancock 1981). Management measures include licence limitation, fitting of escape gaps on all pots, return to the sea of all undersize (carapace length less than 76 mm) and berried rock lobsters, seasonal closures, etc. (Hancock 1981).

The main life history stages of the western rock lobster have been described in Phillips et al. (1980), Hancock (1981), and Morgan et al. (1982). They consist of the following: (a) phyllsoma larvae hatching from eggs in spring–summer (September–January); (b) after a 9- to 11-mo planktonic phase, metamorphosis of the phyllosoma larvae into the puerulus stage which settles on the inshore reefs; (c) the juvenile stage of the 2- to 5-yr-olds where they generally remain on the inshore reefs; (d) migration of the recently moulted, light

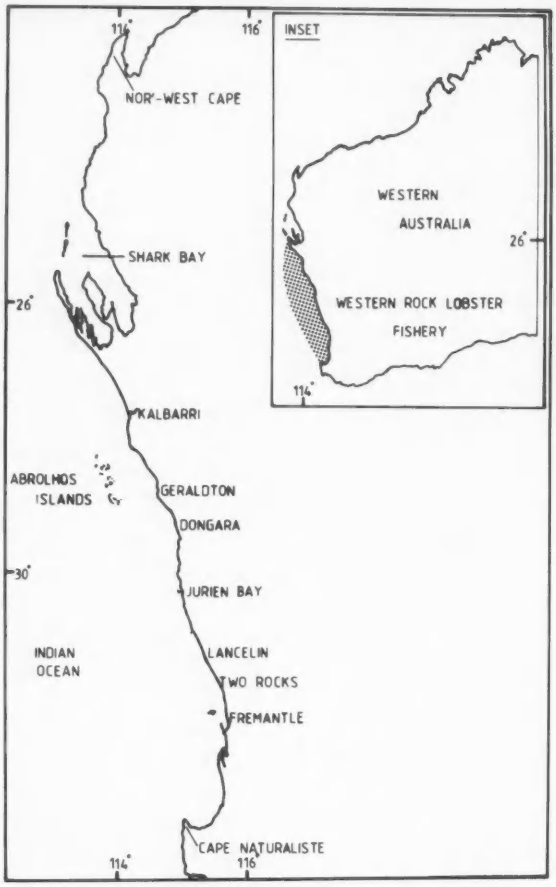


FIG. 1. Area of operation of the western rock lobster fishery and locations from which the monitoring of the commercial fishery is undertaken.

coloured, immature animals (mainly 5 yr old) from the inshore reefs to deeper waters during November–January; (e) mating during winter and spring (June–November).

Since 1969, management of the fishery has been aided by the use of an estimate of the abundance of puerulus settlement to predict the level of recruitment to the fishery 4 yr later (Morgan et al. 1982; Phillips 1986). This relationship has proved useful in providing fishermen and fisheries managers with forecasts of the catch for a series of seasons. This has enabled management options to be examined up to 4 yr in advance of the subsequent recruitment to the fishery of a year-class. It has also enabled fishermen and their financers to make decisions with some knowledge of possible trends in the fishery during the next 4 yr. Morgan et al. (1982) also examined the relationship between juveniles (2- to 4-yr-olds) and recruits to the fishery, but this did not provide a suitable basis for predicting recruitment to the fishery. The index of juvenile abundance used in that study was based on mark–recapture data from nursery reefs at two locations.

Whilst the variation in catches between seasons is not high compared with other fisheries, the high capital investment by fishermen means that even variations as low as 20% can cause financial hardship and so are worth knowing in advance. In addition the very high levels of effort under which the fishery is currently operating give rise to concern regarding the level of spawning stock that can be maintained with fluctuations in the level of recruitment.

Determining the spawning stock–recruitment relationship is of prime importance in the management of a fishery (Gulland 1973); however, Hancock (1973) mentioned that little information was available on stock–recruitment for crustaceans. Since then, there have been a number of reports including Morgan et al. (1982) for rock lobsters, Botsford and Wickham (1978), McKelvey et al. (1980), and Tang (1985) for crabs, and Penn and Caputi (1985) for prawns. For longer lived species such as rock lobster, there may be a greater likelihood of recruitment to the fishery being affected by density-dependent effects on mortality (Chittleborough 1970; Morgan 1974; Chittleborough and Phillips 1975) and growth as well as environmental effects. It would, therefore, assist in developing an insight into these density-dependent and environmental processes and be beneficial to the management of this very important fishery to monitor the juvenile year-classes prior to recruitment to the fishery.

In this paper, indices of juvenile (3- and 4-yr-old) abundance, based on a commercial monitoring program at sea, are estimated and then related to the level of their recruitment to the fishery.

## Methods

The convention adopted in this paper to describe rock lobster year-classes is similar to that used by Morgan et al. (1982) with the year-classes denoted by the time of hatching. For example, the 1970–71 year-class refers to eggs that hatched during 1970–71. Puerulus settlement occurred 9–11 mo later in 1971–72, and 3- and 4-yr-old juveniles were present in 1973–74 and 1974–75, respectively, and recruited to the fishery as 5-yr-olds in 1975–76.

### Abundance of Juveniles

The indices of juvenile abundance are based on length frequency data obtained from a commercial monitoring program which commenced in the 1971–72 season. Data collected onboard include: (a) number of pots sampled, (b) carapace length (1-mm interval) measurements for males and females, (c) pot soak time, and (d) pot type. These data are obtained from four locations (Dongara, Jurien Bay, Lancelin, and Fremantle, see Fig. 1) for each month of the fishing season (currently 15 November – 30 June) and for four depth categories (0–18, 18–36, 36–54, and over 54 m at each of the four locations).

The catch rates (number caught per pot lift) of undersize animals between 68 and 76 mm provided the basis for an index of abundance of 4-yr-old juveniles, and those less than 68 mm provided the basis for an index of 3-yr-old juveniles, since 2-yr-olds rarely enter pots (Chittleborough 1970). This corresponds with an annual growth increment of about 10 mm for 3- and 4-yr-old juveniles (Chittleborough 1976).

The index was calculated from a multiple regression (stepwise) of logarithmically transformed 3- and 4-yr-old catch rates (weighted by the number of pots providing the sample) with the following factors: year, month, location, sublocations, depth, soak time, and moon illumination as determined from Austin et al. (1976). The back-transformed regression coefficients associated with the factor "year" provided the index of juvenile

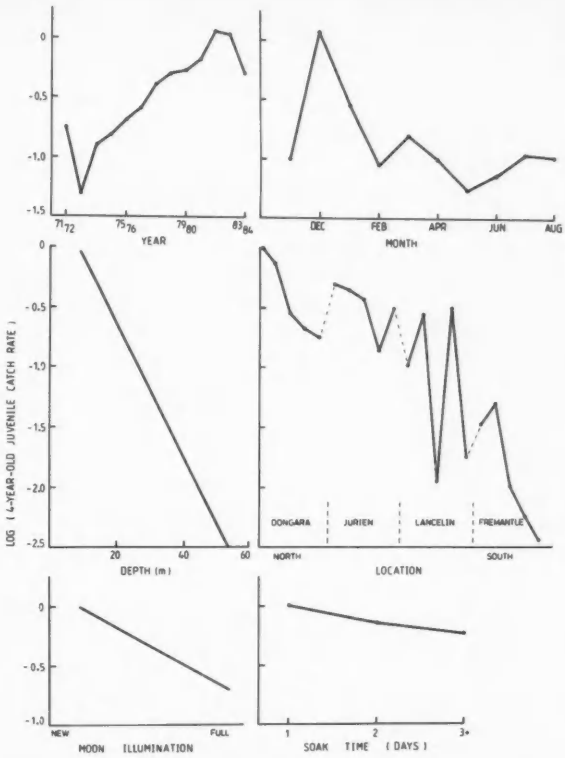


FIG. 2. Parameters of the factors used in the multiple regression of the logarithmically transformed 4-yr-old juvenile catch rates.

abundance which was standardized for the other factors affecting the catch rates. This approach using regression/ANOVA modelling in the standardization of catch rates, i.e. relative abundance indices, is similar to that discussed by Gulland (1956) and further developed and used by Robson (1966), Kimura (1981), Gavaris (1980), and others. An interesting feature of this method of obtaining relative abundance indices is that every time the multiple regressions are rerun with the addition of another year's data, then all the parameters are recalculated, including the parameters representing the indices of abundance of the previous years.

### Abundance of Recruits to the Fishery

Morgan et al. (1982) used catch divided by fishing effort from the November–December data of the fishermen's monthly returns as the Morgan recruitment index. These data consist of catch and effort by month, which must be provided by all fishermen as a condition of their fishing licence. The November–December period was chosen, since it corresponds to the time of migration of newly moulted, pale-coloured rock lobsters from the inshore reefs to deeper waters. These animals are generally 4–6 yr old (mainly 5 yr) and most would be new recruits to the fishery having just attained legal size.

A revised index of recruitment has been developed which uses rock lobster research logbook data in which daily catch and effort (potlifts) are recorded by four depths. Logbook data are supplied voluntarily by 20–30% of the skippers from all areas of the fishery. This revised index was based on logarithmically transformed catch rates in depths 0–18 m over the latitudes 28–32°S using only pots of one day soak time. A 7-d moving average was then used to smooth out daily fluctuations in catch rate, and the highest back-transformed catch rate over a 60-d period during the time of recruitment November–January was chosen as the index. Thus, this index allows for the possibility that the timing of the recruitment may vary between years.

TABLE 1. Recruitment indices and total catch related to a given year-class. *Preliminary estimates.

| Year-class | Recruitment index: Year | Morgan | Revised | Total catch ($m \cdot kg^{-1}$) |
|---|---|---|---|---|
| 1968–69 | 1973–74 | 0.67 | 0.53 | 6.8 |
| 1969–70 | 1974–75 | 1.00 | 0.67 | 8.3 |
| 1970–71 | 1975–76 | 1.12 | 0.70 | 8.7 |
| 1971–72 | 1976–77 | 1.08 | 0.64 | 9.3 |
| 1972–73 | 1977–78 | 1.24 | 0.76 | 10.1 |
| 1973–74 | 1978–79 | 1.44 | 0.92 | 11.4 |
| 1974–75 | 1979–80 | 1.36 | 0.76 | 10.7 |
| 1975–76 | 1980–81 | 1.06 | 0.70 | 9.9 |
| 1976–77 | 1981–82 | 1.40 | 0.88 | 10.6 |
| 1977–78 | 1982–83 | 1.68 | 0.90 | 12.4 |
| 1978–79 | 1983–84 | 1.41 | 0.96 | 10.7 |
| 1979–80 | 1984–85 | 1.20* | 0.74* | 9.5* |

TABLE 2. Correlations (and proportion of variance explained in parentheses) between the logarithmic transformation of 3- and 4-yr-old juvenile indices (male, female, and combined) with logarithmic transformation of the Morgan and revised recruitment indices.

| Juvenile indices | Recruitment indices: Morgan | | Revised | |
|---|---|---|---|---|
| 3-yr-old males | 0.88 | (0.75) | 0.95 | (0.89) |
| 3-yr-old females | 0.86 | (0.71) | 0.90 | (0.79) |
| 3-yr-old combined | 0.86 | (0.71) | 0.92 | (0.83) |
| 4-yr-old males | 0.92 | (0.82) | 0.93 | (0.84) |
| 4-yr-old females | 0.89 | (0.76) | 0.90 | (0.79) |
| 4-yr-old combined | 0.90 | (0.79) | 0.92 | (0.82) |

## Results

### Abundance of Juveniles

Figure 2 displays the values of the parameters from the multiple regression of the logarithmically transformed 4-yr-old juvenile catch rate. The greatest amount of variation in catch rate is associated with the factors "depth" and "location." Juvenile catch rates decrease from northern to southern locations and with increasing depth. The factor "month" shows a drop in the catch rates during November, February, and May and these correspond to periods of moulting. There are also slightly lower catch rates associated with the full moon and increasing soak time of the pots.

Because the escape gap used for the 1971–72 season was 51 mm compared with the 54 mm used for 1972–73 onward, the estimate of 4-yr-old juveniles for 1971–72 has not been used. The index of 3-yr-old juveniles for 1971–72, i.e. 1968–69 year-class, was estimated from the index of 4-yr-old juveniles in 1972–73 using regression analysis.

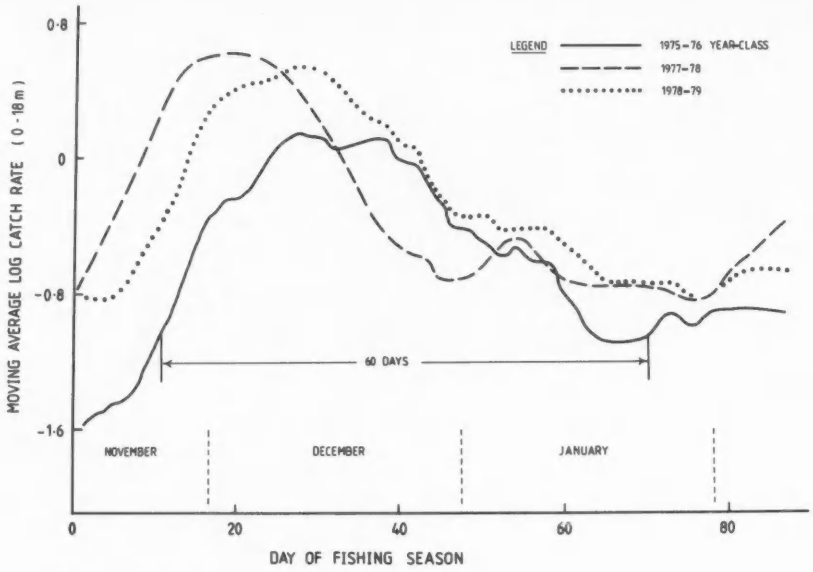


FIG. 3. Seven-day moving average of the logarithm of the daily commercial catch rate (kilograms per potlift) for three year-classes by the day of the season, which starts on 15 November. The 60 d used for the revised recruitment index for the 1975–76 year-class is shown.

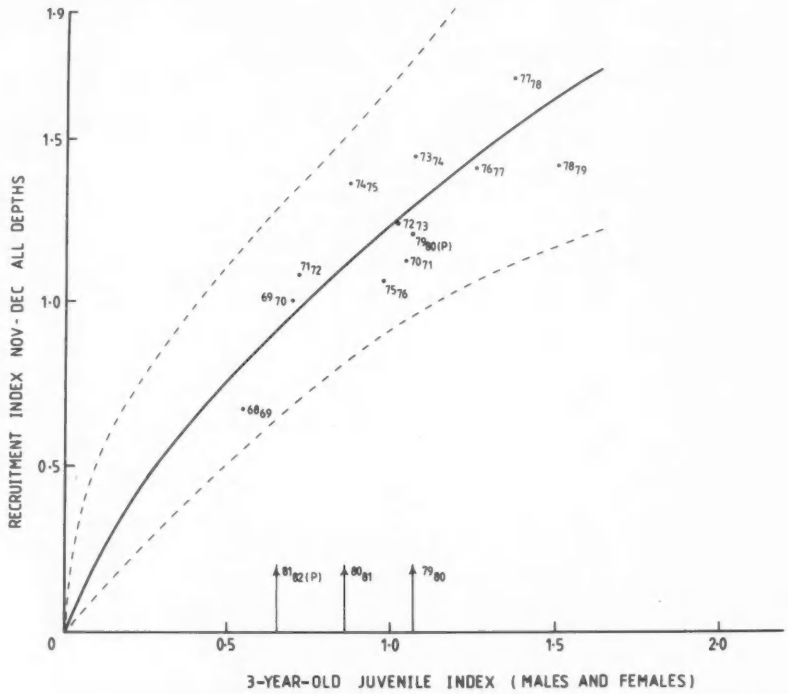


FIG. 4. Relationship with 95% confidence limits for the individual points between the index of the 3-yr-old juveniles (males and females combined) with the Morgan recruitment index. The spawning season of the year-class is shown. Arrows on the *x*-axis indicate prediction of recruitment of the year-classes; P indicates preliminary estimate.

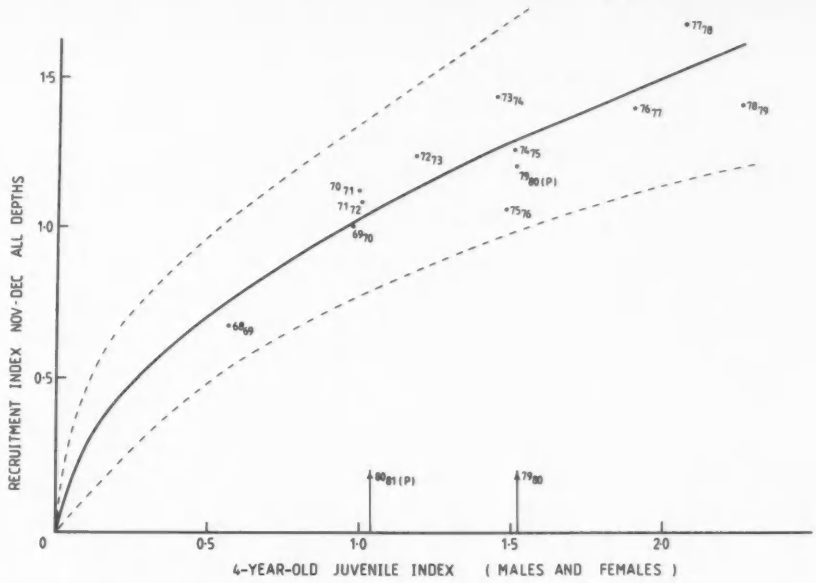


FIG. 5. Relationship with 95% confidence limits for the individual points between the index of the 4-yr-old juveniles (males and females combined) with the Morgan recruitment index. The spawning season of the year-class is shown. Arrows on the *x*-axis indicate prediction of recruitment of the year-classes; P indicates preliminary estimate.

In order to improve the precision of the year-to-year variation in the 4-yr-old juvenile index, the interaction between depth with location, month, and soak time was also added to the multiple regression, since it added a further 5% to the variance explained.

## Abundance of Recruits to the Fishery

The Morgan recruitment index (MRI), the revised recruitment index (RRI), and the total catch for the western rock lobster fishery are shown in Table 1 for the year-classes 1968–69 to 1978–79. The correlations between the indices with the catch (tonnes) during the season were 0.97 and 0.89, respectively, after logarithmic transformation of catch and recruitment indices. The relationships were

$$\text{Catch} = 8.71\text{MRI}^{0.654}, \qquad \text{Catch} = 12.30\text{RRI}^{0.817}.$$

Some examples of the 7-d moving average of the log catch rates, on which the revised recruitment index is based, are shown in Fig. 3. This indicates that a clear peak in recruitment is obtained during November–December, the period of migration of the newly moulted lobsters. However, in some years this peak occurs in late November – early December (e.g. 1977–78 year-class) whilst in other years it occurs during late December and extends into January.

## Juvenile to Recruits Relationship

The relationships with 95% confidence limits for individual points between 3- and 4-yr-old juvenile indices ($J_3$ and $J_4$, respectively, males and females combined) and the Morgan recruitment index have been fitted using a power curve (i.e. a log–log equation) which resulted in correlations of 0.86 and 0.90, respectively (Table 2; Fig. 4 and 5), with the following equations:

$$\text{MRI} = 1.0249J_3^{0.5499}, \qquad \text{MRI} = 1.2139J_4^{0.6920}$$

The estimates of the 3- and 4-yr-old juvenile indices for the 1979–80 year-class are shown (arrowed) on the juvenile index axis in Fig. 4 and 5, respectively. A preliminary estimate of the corresponding recruitment index for this year-class indicates a good fit between the predicted value of the recruitment with the actual recruitment index. This year-class has not been used in the regression equation to determine the relationship and so represents an unbiased check on the prediction. The predictions of recruitment from the 1980–81 and 1981–82 year-classes are also indicated in Fig. 4 and 5. Using the 3-yr-old juvenile index in Fig. 4 as an example, the predicted Morgan recruitment indices for the year-classes 1979–80, 1980–81, and 1981–82 are 1.27, 1.10, and 0.91, respectively. These values then correspond to predicted catches of 10.2, 9.3, and 8.2 million kg, respectively.

The correlations between the 3- and 4-yr-old indices and both the Morgan and the revised recruitment index are shown in Table 2. No significant difference is evident between the correlations although in all cases the correlations involving the revised recruitment index were higher than those with the Morgan index. Also, correlations with the 3- and 4-yr-old juvenile indices using males resulted in higher correlations compared with females. Whilst these differences in correlations need to be further evaluated, since only 11 year-classes are available, it would still be worthwhile to further examine the relationships which account for most of the variation.

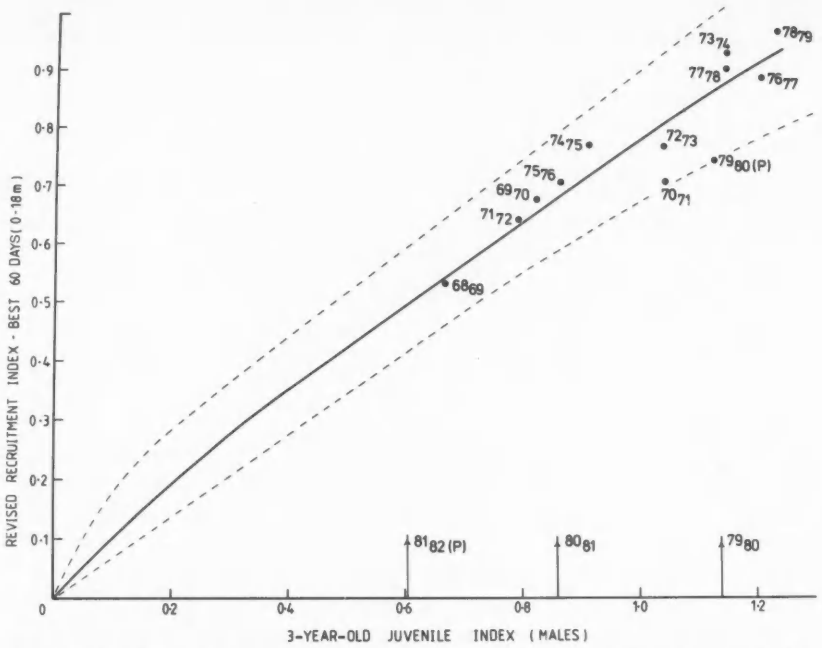


FIG. 6. Relationship with 95% confidence limits for the individual points between the index of the 3-yr-old male juveniles with the revised recruitment index. The spawning season of the year-class is shown. Arrows on the *x*-axis indicate prediction of recruitment of the year-classes; P indicates preliminary estimate.

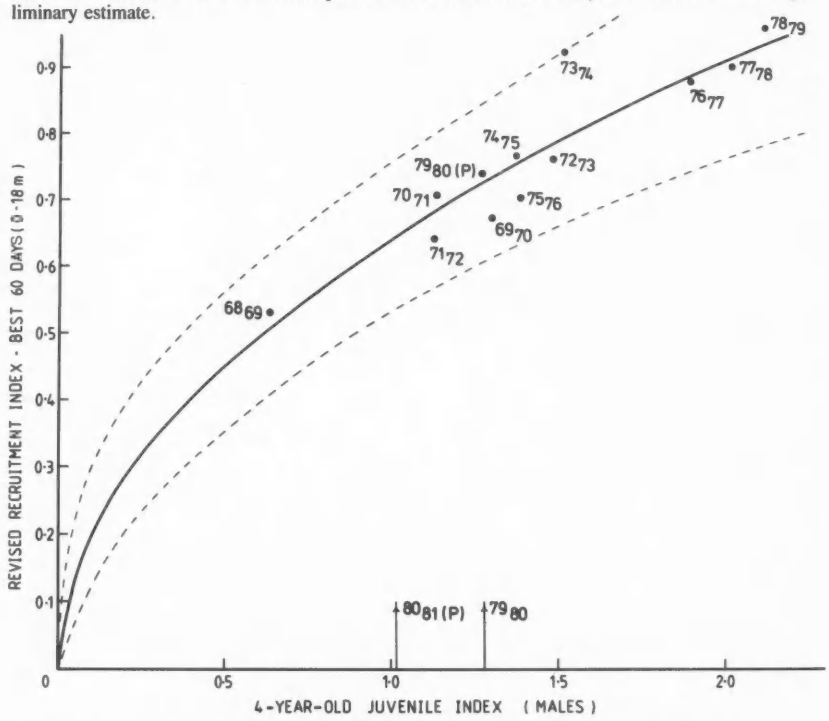


FIG. 7. Relationship with 95% confidence limits for the individual points between the index of the 4-yr-old male juveniles with the revised recruitment index. The spawning season of the year-class is shown. Arrows on the *x*-axis indicate prediction of recruitment of the year-classes; P indicates preliminary estimate.

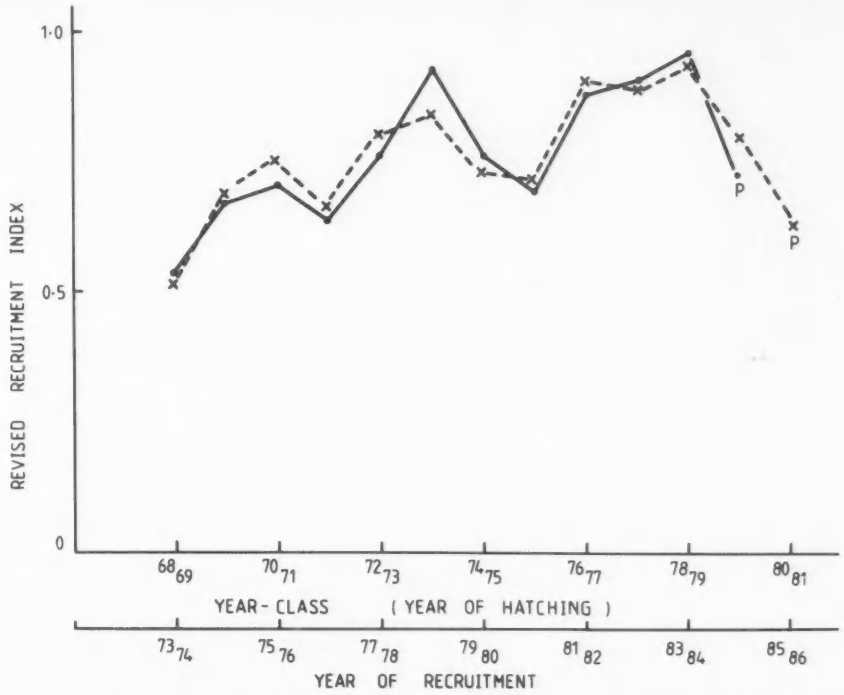


FIG. 8. Relationship between the revised recruitment index (solid line) and its predicted value (broken line) from the multiple regression analysis using both the 3- and 4-yr-old male juvenile indices. P indicates preliminary estimate.

The relationships between the 3- and 4-yr-old male juvenile indices ($JM_3$ and $JM_4$, respectively) and the revised recruitment index resulted in correlations of 0.95 and 0.93 with the following equations (Fig. 6 and 7):

$$RRI = 0.7676JM_3^{0.8618}, \qquad RRI = 0.6372JM_4^{0.4991}$$

with the standard errors of the slopes being 0.09484 and 0.06705, respectively, both significant at the 0.001 level. These equations represent the improvements in the relationship due to changes in both the juvenile and recruitment indices. The predicted recruitment from the 1979–80 year-class and the expected recruitment from the 1980–81 and 1981–82 year-classes indicate a similar decreasing trend to those shown in Fig. 4 and 5.

Multiple regression was also utilised to examine the effect of simultaneously using both 3- and 4-yr-old male juvenile estimates from the same year-class to predict recruitment to the fishery. This resulted in a multiple correlation of 0.97 with the following equation:

$$RRI = 0.7072JM_3^{0.5341} JM_4^{0.2223}$$

with the standard errors of the slopes being 0.1592 and 0.09437 for the 3- and 4-yr-old indices, respectively.

Figure 8 shows a good fit between the revised recruitment index with its predicted value from the multiple regression. For the 11 year-classes used to determine the relationship (1968–69 to 1978–79), the percentage difference between the actual and predicted value ranged from 0 to 8.7% with a mean of 3.4%. For the 1979–80 year-class not used in determining the relationship, the predicted decrease was borne out with an 8.1% difference between the predicted and the preliminary estimate of the revised recruitment index.

## Discussion

Even though the relationships between 3- and 4-yr-old juveniles and the recruits to the fishery are based on only 11 yr of data, the high correlations found suggest a good relationship. The 3- and 4-yr-old juvenile indices provide a means of predicting recruitment to the fishery 2 and 1 yr in advance, respectively, thereby providing an independent check on the predicted recruitment based on the puerulus settlement. Preliminary analysis suggest that 3- and 4-yr-old juveniles generally have a higher correlation with both the Morgan and revised recruitment index than does the puerulus index, though the puerulus index has the higher correlation with total catch (Phillips 1986).

In general, the 11 year-classes used to establish the multiple regression relationship between the revised recruitment index with the 3- and 4-yr-old male juvenile indices, as well as the year-class (1979–80) which is used to predict the latest recruitment, show a good fit between predicted and actual recruitment (Fig. 8). Since this relationship utilises the 4-yr-old male juvenile index, prediction can only be made 1 yr in advance. The predicted recruitment from the 1980–81 year-class, recruiting to the fishery in 1985–86, predicts a decrease in recruitment which could be the lowest since the 1968–69 year-class. To examine the prediction 2 yr in advance, only the relationship between recruitment index and the 3-yr-old juvenile index can be utilised. This relationship suggests that the recruitment from the 1981–82 year-class will be even lower

than that obtained from the 1968–69 year-class (Fig. 6), making it the lowest recruitment during the last 15–20 yr. However, Phillips (1986) suggests that this decreasing trend in recruitment is likely to be reversed, since good puerulus settlement has occurred since the 1981–82 year-class and preliminary observations from the juvenile catch agrees with this assessment. The relationship between the recruitment indices and catch is generally good and an expected decrease or increase in recruit index should be accompanied by similar changes in the total catch. However, care needs to be exercised, since the role of variations in fishing power and effective effort between years still needs to be assessed.

With most of the variation in the recruitment indices being explained by the juvenile estimates, there appears to be no evidence of environmental factors strongly affecting recruitment after the juvenile stage. Also, the almost linear relationship between the life history stages suggests that density-dependent mortality for the 3- and 4-yr-old juveniles is not very strong. This is in contrast with the density-dependent mortality noted by Chittleborough and Phillips (1975).

The use of regression analyses on the juvenile catch rates enables standardization of the annual estimates of the juvenile indices with respect to other factors. The need for this is clear from the variation in the juvenile catch rates evident for some of the factors such as depth, month, and location (see Fig. 2). However, other factors which may affect these estimates have not been taken into account at this stage. These include the increase in efficiency of the fishing fleet by the use of larger pots, colour echo sounders, radar, etc. These factors would tend to result in an overestimate of the juvenile and recruitment indices for the later years compared with the earlier years in Fig. 3–6. The significance of these factors is being investigated with a view to providing appropriate corrections. Also, a revision on the size-classes used to provide the estimates of juveniles may also be required, since there are time, location, and sex differences in growth which should be taken into account. Another factor which may affect the use of catch rates as indices of abundance is the change in total fishing effort in the fishery during the period. There has been some increase in effort over the period, which may have caused the catch rates to decrease; however, the catch rates have generally increased, indicating that total effort is not having a marked effect.

The improvement in the juvenile/recruitment correlation when males only were used for the juvenile indices may be due to the generally higher proportion of males retained by the pots for each carapace length category compared with females (Brown and Caputi, unpubl. data) or because the size-classes used to determine the age-classes may be more representative of males than females.

A higher correlation of juveniles to recruits was obtained using the revised recruitment index compared with the Morgan recruitment index. This may be due to the Morgan recruitment index being based on some animals, caught in November–December, especially in deeper waters (say greater than 36 m), which are too large to have moulted to legal size in the current season (Brown and Barker 1985), whereas the abundance of the smaller legal size animals in the shallow waters (Brown and Barker 1985) would more accurately reflect the abundance of recruits. Also, in some years the period of recruitment occurs later and extends into January so that the November–December period (used by Morgan et al. 1982) does not take into account the full period of recruitment (e.g. 1975–76 year-class in Fig. 4 and 5). The higher correlation of the Morgan recruitment index with catch is due to this index being based on catches of all depths which would include the lobsters which were not caught during the year they first recruited into the fishery. The revised index, while still correlating well with the total catch, is more representative of the new recruits to the fishery.

The number of juveniles caught is, of course, dependent on the escape gap being used (currently 305 × 54 mm). A change in the length of the escape gap has been recommended (Brown and Caputi 1986), and a correction will need to be applied to make the data sets before and after the escape gap changes compatible, since the catch rates of undersize lobsters may be reduced by 40–60%. This could affect the precision of the later juvenile estimates.

The juvenile estimates can provide intermediate checks on the abundance of a year-class between the puerulus and recruitment stages and to forecast recruitment to the fishery. Fisheries managers and fishermen could utilise these predictions in their consideration of management options in response to fluctuations in recruitment. For example, when a low recruitment is expected, as is likely in 1986–87 (from predictions for the 1981–82 year-class) (see Fig. 4 and 6), management measures could be taken from the beginning of the season to ensure that the breeding stock was not placed in jeopardy, rather than having to wait for the season to be half completed to obtain a measure of recruitment before taking action to protect the potential breeding stock. In addition, the ability to accurately forecast recruitment would allow improved financial planning by fishermen.

## Acknowledgements

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## References

AUSTIN, R. H., B. F. PHILLIPS, AND D. J. WEBB. 1976. A method for calculating moonlight illuminance at the earth's surface. J. Appl. Ecol. 13(3): 741–748.

BOTSFORD, L. W., AND D. E. WICKHAM. 1978. Behaviour of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*). J. Fish. Res. Board Can. 35: 833–843.

BOWEN, B. K. 1980. Spiny lobster fishery management, p. 243–264. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol II. Academic Press, New York, NY. 390 p.

BROWN, R. S., AND E. H. BARKER. 1985. The western rock lobster fishery 1982–83. West. Aust. Dep. Fish Wildl. Rep. 70: 23 p.

BROWN, R. S., AND N. CAPUTI. 1986. Conservation of recruitment of the western rock lobster (*Panulirus cygnus*) by improving survival and growth of undersize rock lobsters captured and returned by fishermen to the sea. Can. J. Fish. Aquat. Sci. 43: 2236–2242.

CHITTLEBOROUGH, R. G. 1970. Studies on recruitment in Western Australian rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. Aust. J. Mar. Freshwater Res. 21: 131–148.

1976. Growth of juvenile *Panulirus longipes cygnus* George on coastal reefs compared with those reared under optimal environmental conditions. Aust. J. Mar. Freshwater Res. 27: 279–295.

CHITTLEBOROUGH, R. G., AND B. F. PHILLIPS. 1975. Fluctuations of year-class strength and recruitment in the western rock lobster *Panulirus longipes* (Milne-Edwards). Aust. J. Mar. Freshwater Res. 26: 317–328.

GAVARIS, S. 1980. Use of a multiplicative model to estimate catch rate and effort from commercial data. Can. J. Fish. Aquat. Sci. 37: 2272–2275.

GULLAND, J. A. 1956. On the fishing effort in English demersal fisheries. Fish. Invest. Ser. II, Vol 20(5): 1–41.

1973. Can a study of stock and recruitment aid management decisions? Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 368–372.

HANCOCK, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 113–131.

1981. Research for management of the rock lobster fishery of Western Australia. Proc. Gulf Caribb. Fish. Inst. 33: 207–229.

KIMURA, D. K. 1981. Standardised measures of relative abundance based on modelling log (C.P.U.E.), and their application to Pacific Ocean perch (*Sebastes alutus*). J. Cons. Int. Explor. Mer 39: 211–218.

MCKELVEY, R., D. HANKIN, K. YANOSKO, AND C. SNYGG. 1980. Stable cycles in multistage recruitment models: an application to the Northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37: 2323–2345.

MORGAN, G. R. 1974. Aspects of the population dynamics of the western rock lobster, *Panulirus cyngus* George. I. Estimation of population density. Aust. J. Mar. Freshwater Res. 25: 235–248.

1980. Population dynamics and management of the western rock lobster fishery. Mar. Policy 4: 52–60.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia. Fish. Bull. 80(3): 475–486.

PENN, J., AND N. CAPUTI. 1985. Stock–recruitment relationships for the tiger prawn (*Penaeus esculentus*) fishery in Exmouth Gulf, Western Australia, and their implications for management. *In* P. C. Rothlisberg, B. J. Hill, and D. J. Staples [ed.] Second Australian National Prawn Seminar, NPS2, Cleveland, Australia.

PHILLIPS, B. F. 1986. Prediction of commercial catches of the western rock lobster *Panulirus cygnus*. Can. J. Fish. Aquat. Sci. 43: 2126–2130.

PHILLIPS, B. F., G. R. MORGAN, AND C. M. AUSTIN. 1980. Synopsis of biological data on the western rock lobster *Panulirus cygnus* George, 1962. FAO Fish. Synop. 128: 64 p.

ROBSON, D. S. 1966. Estimation of the relative fishing power of individual ships. ICNAF Res. Bull. 3: 5–14.

TANG, Q. 1985. Modification of the Ricker stock recruitment model to account for environmentally induced variation in recruitment with particular reference to the blue crab fishery in Chesapeake Bay. Fish. Res. 3: 13–21.

# Session 3
# Larval Distribution Dynamics

Chairman: B. F. Phillips

*Division of Fisheries Research, CSIRO, P.O. Box 20, North Beach, Western Australia, 6020*

# California Spiny Lobster (*Panulirus interruptus*) Larval Retention and Recruitment: A Review and Synthesis

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Pringle, J. D. 1986. California spiny lobster (*Panulirus interruptus*) larval retention and recruitment: a review and synthesis. Can. J. Fish. Aquat. Sci. 43: 2142–2152.

The late Dr. M. W. Johnson studied *Panulirus interruptus* phyllosome larval natural history from samples collected between 1949 and 1955 inclusive on the California Cooperative Oceanic Fisheries Investigations (CalCOFI) grid. Despite wide broadcasting of larvae, he concluded that gyres and countercurrents must retain larvae to ensure recruitment to the population. The conclusions are reviewed and the data reinterpreted in light of both recent physical oceanographic information and congeneric biology. Phyllosome concentrations are highly aggregated within the California Current: 66% of the larvae were located in 12% of the areal distribution, with the concentrations located off central Baja California. Stage I larvae cooccurred nearshore in areas of moderate Ekman wind drift. They were quickly (about 13 d) transported southward, likely by the California Current, to a perennially occurring, semipermanent gyre. Phyllosome maturation to stage VIII occurred over a 5-mo period within the gyre. Late-stage (IX–XI) concentrations occurred slightly northwest of the gyre, possibly transported by the counterflowing Davidson Current. Pueruli were rarely encountered, suggesting a deepwater (>140 m) distribution. Onshore movement is likely made by the puerulus stage. Phyllosome concentrations in the Southern California Bight were rare (stage IV only). Evidence is presented to support the hypothesis that recruitment to this northern, relatively impoverished brood stock area may be episodic, influenced by the large-scale, interannual El Niño events.

Le regretté Dr M. W. Johnson a étudié l'histoire naturelle des larves de phyllosomes de *Panulirus interruptus* à partir d'échantillons recueillis entre 1949 et 1955 inclusivement, sur une grille des California Cooperative Oceanic Fisheries Investigations (CALCOFI). Malgré une vaste dispersion des larves, il a conclu que des tourbillons océaniques et des contre-courants doivent retenir les larves pour assurer le recrutement dans la population. On examine les conclusions et on réinterprète les données en tenant compte des informations récentes sur l'océanographie physique et la biologie des congénères. Les concentrations de phyllosomes sont très agglomérées à l'intérieur du courant de Californie : 66 % des larves étaient localisées dans 12 % de la distribution superficielle, les concentrations se trouvant situées au large de la partie centrale de la Basse-Californie. Des larves du stade I se retrouvaient ensemble près des côtes dans les secteurs de la dérive modérée due au vent d'Ekman. Elles ont été transportées rapidement (environ 13 j) au sud, vraisemblablement par le courant de Californie, vers un tourbillon océanique semi-permanent se produisant perpétuellement. La maturation des phyllosomes au stade VIII s'est produite sur une période de 5 mo à l'intérieur du tourbillon. Les concentrations des derniers stades larvaires (IX-XI) se sont produites légèrement au nord-ouest du tourbillon, transportées probablement par le courant Davidson qui coule en sens inverse. On a rencontré rarement des pueruli, ce qui laisse supposer une distribution en eaux profondes (>140 m). Le mouvement près de la côte est probablement dû à des individus du stade puerulus. Les concentrations de phyllosomes au sud de la baie de Californie ont été rares (stade IV seulement). Des preuves sont présentées pour appuyer l'hypothèse voulant que le recrutement dans ce secteur nord, relativement pauvre, de reproducteurs soit épisodique, influencé par les phénomènes de grande envergure interannuels du courant El Niño.

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The late Dr. Martin Johnson was one of the cofounders of oceanography's multidisciplinary approach (Svedrup et al. 1942), now an integral part of this science (McGowan and Brinton 1985). He maintained that one cannot separate in situ changes from advective events when studying dynamic oceanic processes. The California Current flora and fauna were frequently found to be a mixture of species of external origin. The concept that physical oceanography has a major influence on plankton biology and ecology was then developed. Johnson (1954) went further when he suggested that physical variables were of even greater influence on plankton population density and community structure than were food limitation, energy flow, and competitive interaction.

Dr. Johnson, late in his career, was challenged by the enigma of the spatial and temporal distribution in the California Current of the California spiny lobster (*Panulirus interruptus* (Randall)) phyllosome larvae. He delivered in the early 1950's a broad and skillful oceanographic background to the study of this problem (McGowan and Brinton 1985). A fixed grid of stations had been set up in 1949 in the California Current by California Cooperative Oceanic Fisheries Investigations (CalCOFI). Biological samples and hydrographic measurements were made monthly (1949–60) from two to three vessels (the stations have been sampled less frequently since 1960). This was the source of Dr. Johnson's data (Johnson 1956, 1960a, 1960b).

Surprisingly, little work has since been done on the phyllosome ecology of *P. interruptus*, given its economic im-

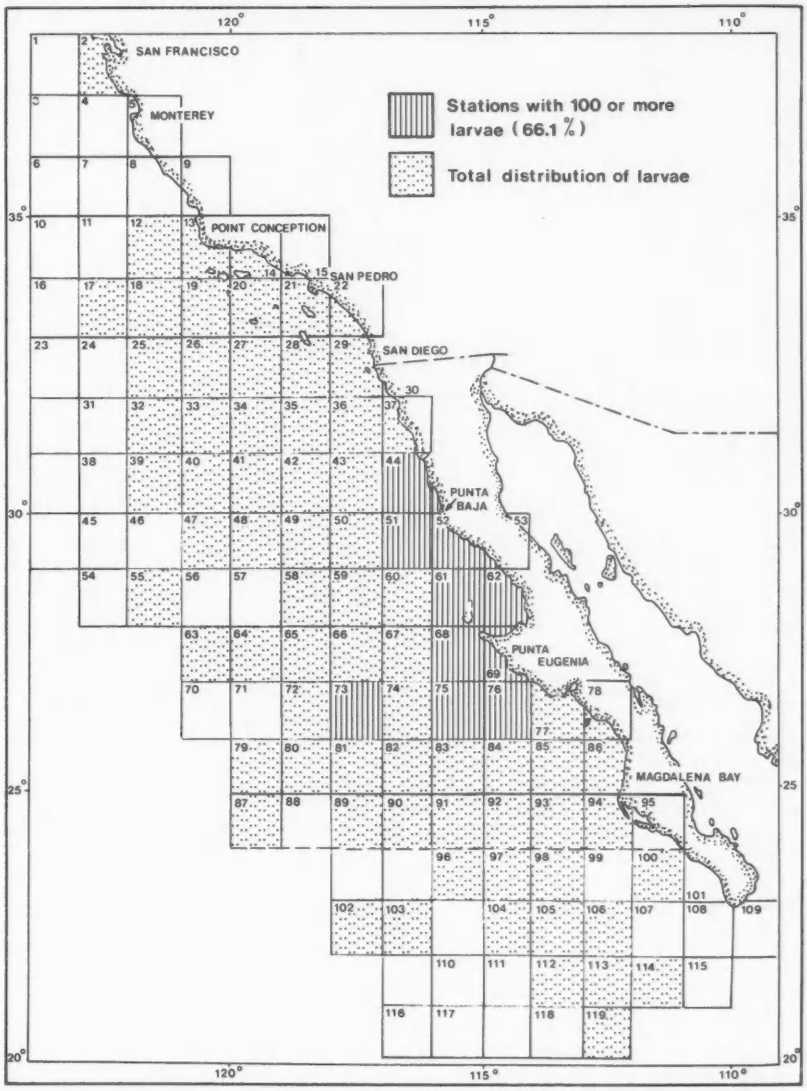


FIG. 1. Distribution of *P. interruptus* phyllosome larvae captured on the CalCOFI grid during 1949–55 inclusive (data from Johnson 1960a). Note that 66.1% of the larvae occurred in 12% of the areal distribution.

portance, particularly in northwestern Mexico. Advances have been made in both the biology of congenerics (particularly *P. cygnus*) and the physical oceanography of the California Current. Dr. Johnson's data and conclusions are reviewed here in the light of this more recent knowledge. Emphasis is placed on extending our understanding of larval retention and recruitment in this system.

## Review of Data, Hypotheses, and Concepts

### Background for Dr. Johnson's Conclusions in Larval Advection

Adult *P. interruptus* ranges from Monteray Bay, California, (rare north of Pt. Conception) to Magdalena Bay, Mexico (Fig. 1); central Baja California (Mexico) is the center of abundance (Johnson 1960a). Commercial exploitation began in 1872 (F. Odemar, California Department of Fish and Game, Long Beach, CA, pers. comm.) and a commercial trap fishery now exists throughout the species range (Duffy 1973). California State lobster fishing regulations were introduced in 1901 (F. Odemar, pers. comm.). Shortly afterward, Allen (1916) appealed for a full biological understanding of this species. Forty years later, Johnson (1956) made a similar appeal after what appeared to be an acceptance of Lindberg's (1955) challenge that the larvae were the "... keystone of the population ... and about the larval stage little is known."

CalCOFI personnel collected hundreds of plankton samples.

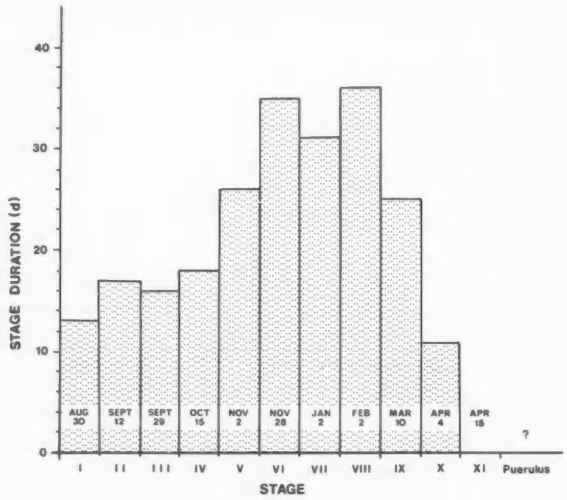


FIG. 2. Estimated stage duration and temporal occurrence of *P. interruptus* phyllosome larvae (data from Johnson 1960a).

Hauls were made with a conical net, 1 × 5 m, with mesh apertures of 0.65 mm, finer at the codend. Tows were made from depth (from 70 m before 1951 and from 140 m after 1951) at a rate of approximately 14 m·min$^{-1}$, with a tow angle of 45°. Samples from 75 cruises between 1949 and 1955 (inclusive) were sorted and 3287 phyllosomes recovered (Johnson 1960a, 1960b). These low numbers tended to refute Lindberg's (1955) contention that the larvae must be common given the large reproductive potential of the species. Eleven "... rather poorly defined stages ..." were described (Johnson 1956), of which "The intermediate stages are not always clear-cut ... The first, second, tenth and eleventh stages are ... well defined." (Johnson 1960b). Stage duration is plotted with time (Fig. 2). Johnson (1960a) concluded that the time to metamorphosis (puerulus stage) was approximately 230 d. He attempted to discern recruitment processes by plotting horizontal larval distribution with geostrophic flows (steric height data were collected simultaneously with the larvae).

Little was known in the 1950's about the vertical distribution of palinurid larvae. Johnson (1956) suggested that the scarcity of the larvae may indicate a tendency to seek levels near the bottom. Indeed, he noted that a bottom drag had captured a number of stage I's near shore. Lindberg (1955) claimed that Scripps' personnel captured more phyllosomes between 200 and 1200 fathoms than at the surface (unpubl. data). Similarly, Gurney (1936) claimed that the "Thor" and "Discovery" samples exhibited only late-stage phyllosomes ("... high sea forms ...") which were "... apparently confined to the deeper layers ...." Other workers, however, suggested that phyllosomes of the rock lobster, *P. vulgaris*, were either surface dwelling (Cunningham 1892) or exhibited diurnal vertical movement, being more frequent at the surface during darkness (Russel 1923–25). Harada (1957) noted that *P. japonica* phyllosomes were more abundant at the surface at dawn and less abundant after sunrise. Johnson (1960b) noted that 57% of the larvae were captured during darkness. Given this, and the observations from closely related taxa, he concluded that diurnal, vertical migration likely takes place, presumably from below 140 m.

The California Current (~80 km wide) (Bernal 1981) presented a puzzling physical oceanographic picture to observers as early as 1909 (see Reid 1982). Reid admitted that even to the 1950's, physical oceanography was primitive. For example, the data base was even insufficient to predict the appropriate scale for studies! Frequently, biological oceanographic data gave one a better grasp of the distribution of physical anomalies than did the physical data. For example, Allan (1945), studying planktonic diatom distribution around the Channel Islands, noted outstanding spatial and temperal peculiarities which had remained undetected by routine physical methodologies. It was known, however, that wind-generated Ekman transport moved nearshore surface waters offshore. As well, it was generally believed that the surface waters of the California Current moved to the south and southwest and that there was a counterflowing current, the Davidson Current (Johnson 1960b). Initially, Johnson (1960a) concluded that larvae that "... float about with prevailing currents like so many drift bottles ... must result in an enormous loss to the larval population because it (the southward flow and Ekman transport) carries many larvae out to areas unsuitable for metamorphosis and survival." Later, Johnson and Brinton (1963) suggested that comparing animate larvae to inanimate drift bottles may lead to the wrong conclusions. For example, the scenario was given where diurnal, vertically migrating larvae may reduce horizontal advection by riding two counterflowing currents. This later insight supported Johnson's (1960b) earlier conclusion, based on a relatively stable fishery, that "... a system of larval retention sufficient to enable recruitment ..." must be in effect. He ultimately concluded that "Recruitment of lobsters on the coast of southern California and Baja, California must depend upon the development of large eddies, swirls, and counter currents, which retard the flushing out of larvae to the south with the California Current. It is important to discover how this is accomplished and what variability there might be in the system."

## Current Concepts of Physical Oceanography of the California Current

The CalCOFI data suggest the long-term circulation off California is dominated by the equatorward flowing California Current which has typical eastern boundary current characteristics (Winant and Bratokovich 1981). During spring and summer stratification, the surface and bottom currents are opposed, with the near surface waters directed equatorward with a mean velocity of 6.2 cm·s$^{-1}$. The mean current at approximately 29 m is directed northward at a velocity of 4.1 cm·s$^{-1}$ (Winant and Bratokovich 1981). However, according to Bernstein et al. (1977), this straightforward picture of mean circulation in geostrophic balance is rarely realized. For example, in January 1965, based on CalCOFI analysis, the California Current resembled a meandering jet (150 km wide) flowing 20–40 cm·s$^{-1}$ (Bernstein et al. 1977). They concluded "The consistent picture developed ... is that the California Current is an unstable flow, continuously developing meanders with wavelengths of several hundred kilometers, which can intensify over several months and go to cut off, creating isolated eddies." For example, Mooers and Robinson (1984) recently reported a jet 40 km wide moving at 50 cm·s$^{-1}$ to the northwest. They plotted several jets and eddies between March and August 1982 which changed on a scale of weeks.

An interesting marriage of biological and physical data from the CalCOFI time series was summarized by Chelton et al. (1982). The study provided a better understanding of the frequencies and influence of El Niño events on California Current biology. They accounted for much of the variability in zooplankton abundance, not with wind-driven, locally forced Ekman flow but with low-frequency, large-scale, interannual (>608 d) variability in the geostrophic flow (El Niño events). For example, there was strong equatorward transport between 1953 and early 1957, and poleward transport thereafter to 1960.

Chelton et al. (1982) concluded that "El Niño is associated with anomalously warm water in the tropics and positive California sea level anomalies which correspond to anomalous poleward flow. Correspondingly, negative El Niño events are associated with low California sea level and anomalous equatorward flow."

Other persistent physical oceanographic features that might be of importance to the horizontal distribution of *P. interruptus* larvae are the Southern California Eddy (SCE), the nearshore meeting of the zones of convergence and divergence at Punta Eugenia, central Baja (Owen 1980), and the gyre south of Punta Eugenia. The complex of Channel Islands and associated banks are capable of generating and shedding eddies (Owen 1980). The large size (~200 km in diameter) and predictable appearance of the SCE (present annually from 1949 to 1964) (Owen 1980) between July and January was likely the reason Johnson (1960b) suggested its potential as a larval retainer.

The zone of divergence of surface waters generally parallels the coast and extends out to ~250 km where it borders a zone of convergence (Hewitt 1981; Parrish et al. 1981). The confluence of the two zones corresponds to the position of maximum wind stress, the location varying only slightly on a seasonal basis (Parrish et al. 1981). Each and every year they impinge the coast at Punta Eugenia (Parrish et al. 1981). Hewitt (1981) suggested that this likely precludes or dampens poleward movement of water near the coast, and he felt that it may be responsible for the frequent claim that Punta Eugenia is a faunal boundary. Hewitt (1981) also described a persistent eddy south of Punta Eugenia. He suggested that this eddy and the SCE might entrain larvae and act as a recruitment mechanism for long-lived meroplanktonic organisms such as *P. interruptus*. If true, he predicted population differentiation north of San Diego and south of Punta Eugenia.

Parrish et al. (1981) related reproductive strategies of fish in the California Current to physical oceanographic features. They noted the transition zone for cold temperate and warm temperate fauna as the area between Cape Blanco and Pt. Conception. The coast differs spatially and temporally in both Ekman wind drift and upwelling indices (Table 1). The California Bight (Pt. Conception to Punta Eugenia) was "... characterized by minimal offshore Ekman transport [present to a depth of 20 m to 30 m (Parrish et al. 1981)] overlying a geostrophic flow pattern that features a closed gyral circulation near the coast ... and an onshore component of flow farther offshore ... seaward dispersion of reproductive products would appear to be minimized." In support of the latter, they claimed that the more abundant pelagic taxa of the system spawn in this region.

TABLE 1. Qualitative seasonal assessment of Ekman wind drift and upwelling between Cape Mendocino, California, and southern Baja California

| Location | Oceanographic characteristic | Activity per season | | | |
|---|---|---|---|---|---|
| | | Winter | Spring | Summer | Fall |
| Cape Mendocino | Ekman wind drift | Weak nearshore and offshore | Strong nearshore and offshore | Strong nearshore and offshore | Moderate nearshore and offshore |
| Pt. Conception | Upwelling | Weak, some downwelling | Strong | Strong | Weak |
| Pt. Conception | Ekman wind drift | Weak nearshore | Weak nearshore | Weak nearshore | Weak nearshore |
| Punta Baja | Upwelling | Moderate offshore<br>Weak, some downwelling | Strong offshore<br>Strong | Moderate offshore<br>Moderate | Moderate offshore<br>Weak |
| Punta Baja South | Ekman wind drift | Moderate nearshore and offshore | Strong nearshore and offshore | Moderate nearshore and offshore | Moderate nearshore and offshore |
| | Upwelling | Weak | Moderate | Moderate | Weak |

## Conclusions of Physical Oceanography Synopsis

(1) The California Current is an unstable, equatorward flow-

ing eastern boundary current, constantly developing meanders which develop isolated eddies.

(2) There is a poleward flowing counter current, the Davidson Current, which is more pronounced during winter.

(3) There are large-scale interannual events, El Niños, which result in periods of more poleward flow (or reduced southerly transport of the California Current).

(4) Summer and fall Ekman wind drift is strong and moderate, respectively, between Cape Mendocino and Pt. Conception and, for both seasons, is weak between Pt. Conception and Punta Baja and moderate from Punta Baja south. The zone of convergence/divergence of the Ekman windrift is seaward approximately 250 km from Cape Mendocino to San Diego; it impinges the coast between Punta Baja and Punta Eugenia.

(5) There are two regular-occurring mesoscale gyres, one centered in the Channel Islands and the other just south of Punta Eugenia.

## Larval Ecology and Natural History

Johnson (1960a, 1960b) made the following natural history and distributional observations relevant to understanding larval recruitment processes: (1) stage I larvae are hatched inshore from Pt. Conception to Magdalena Bay, Baja California, but the center of production is central Baja California; (2) hatching peaks in August–September (Fig. 2); (3) the phyllosome phase duration is approximately 7.75 mo (Fig. 2); (4) 57% of the larvae were captured at night, suggesting vertical migration; and (5) larvae were rarely taken north of Pt. Conception and south of 24°N. Additionally, stage I and stage XI phyllosomes, respectively, represented 42.5 and 1.2% of the larvae captured. As well, stage longevity ranged from approximately 11 d (stage X) to 36 d (stage VIII). Peaks in stage abundance occurred from late August to mid-April.

Due to the inability to culture panulirid phyllosomes consecutively through all stages, there is little experimental data to verify speculation based on field observations. Dexter (1972) grew *P. interruptus* phyllosomata to stage VI in 60 d. She then speculated that 5 mo might be the approximate total length for the phyllosome phase in situ.

Johnson (1960b) related the horizontal distribution of larvae from selected cruises to prevailing geostrophic flow. This yielded insight into short-term advective processes (sensu Mooers and Robinson 1984), particularly when back-to-back cruises occurred in the same location. Here, in an attempt to uncover phyllosome distribution pattern in relation to longer term physical oceanographic phenomenon, all (1949–55) distributional data were pooled in three stage groups (stage I, stages II–VIII, and stages IX–XI). Stage group concentrations (a concentration is defined as a degree-square (1° longitude × 1° latitude) containing ≥5% of the total number of phyllosomes captured per stage group) were then plotted. The rationale for this approach is, first, certain physical oceanographic features are perennial (Owen 1980; Parrish et al. 1981), second, the persistent, albeit variable, annual recruitment process should involve stable, long-term physical oceanographic features, and, third, phyllosome behavior should have evolved to exploit the latter.

The overall distribution of *P. interruptus* phyllosomes covered 82 degree-squares; however, 66.1% of the captured larvae occupied only 10 degree-squares (Fig. 1). Concentrations of stage I's were coastal, occupying seven degree-squares from San Diego south to Punta Eugenia (Fig. 3). Concentrations of stages II–VIII (which hereafter may be referred to as midstages) are shown in Fig. 4. North of 32°N, concentrations occurred in only three degree-squares, and they were stages III and IV. Stages II–VI were abundant nearshore between 28 and 31°N (to be expected, given the stage I distribution), but even greater concentrations were collected further south to 26°N. Offshore, between 28 and 29°N, small concentrations of stages VI and VIII were found. However, the largest concentrations of the midstage larvae (particularly the later midstages) occurred just south of Punta Eugenia onshore and offshore (Fig. 4). The greatest concentrations of mid- and late- stages occurred between 25 and 28°N in degree-squares 68, 69, 73, 75, 76, and 84; the center of concentration was in the two contiguous degree-squares 68 and 75.

Concentrations of the later larval stages were similar to the midstages but with a more northerly distribution (Fig. 3 and 4). Five of the seven degree-squares were contiguous to, or overlapped, concentrations of stage I (Fig. 3). Overlap of concentrations of all larval stages occurred nearshore off Punta Eugenia (degree-square 68, compare Fig. 3 and 4). A unique feature was the concentration of stages IV–IX offshore about 300 km (degree-square 73) at approximately 116°W and 26°N. Similar concentrations were not observed in adjacent waters.

## Conclusions on Horizontal Larval Advection

(1) Concentrations of phyllosome larvae are rare northwest of 32°N.

(2) Based on the major concentrations of stage I larvae, the brood stock are nearshore at time of larval discharge between 28 and 33°N.

(3) Concentrations of stages II–IV occurred between 28 and 29°N, but major abundances occurred nearshore between 26 and 28°N.

(4) Major concentrations of stages V–VIII were west (offshore) and south (nearshore) of Punta Eugenia from 24 to 28°N.

(5) The center of the major concentrations of stages IX–XI was somewhat north of the center of concentrations of stages V–VIII, but there was considerable overlap (concentrations of all stages occurred nearshore of Punta Eugenia between 27 and 28°N and between 115 and 116°W). Concentrations of stages IX–XI were often contiguous with stage I concentrations.

(6) Over the duration of the phyllosome phase, there was a limited net transport of the larvae south in the direction of the residual current.

## Larval Recruitment in Congenerics

The two most studied congeneric species are *P. argus* and *P. cygnus*. Numerous workers have studied larval ecology of *P. argus* from the Gulf of Mexico, a difficult geographic area to study phyllosome larval ecology. The physical current system is complex (Austin 1972), and it is difficult to distinguish *P. cygnus* phyllosomes from two sympatric congenerics, *P. guttatus* and *P. laevicauda* (Little 1977), and from scyllarid species (Austin 1972). Definitive work on phyllosome vertical distribution is lacking; however, indirect observations (Sims 1966; Sims and Ingle 1966; Austin 1972) suggest that diurnal migration does occur.

Despite the unresolved problems, there has been speculation on the source of Florida *P. cygnus* recruits (Lewis 1951; Ingle et al. 1963; Lyons 1980). However, Menzies and Kerrigan

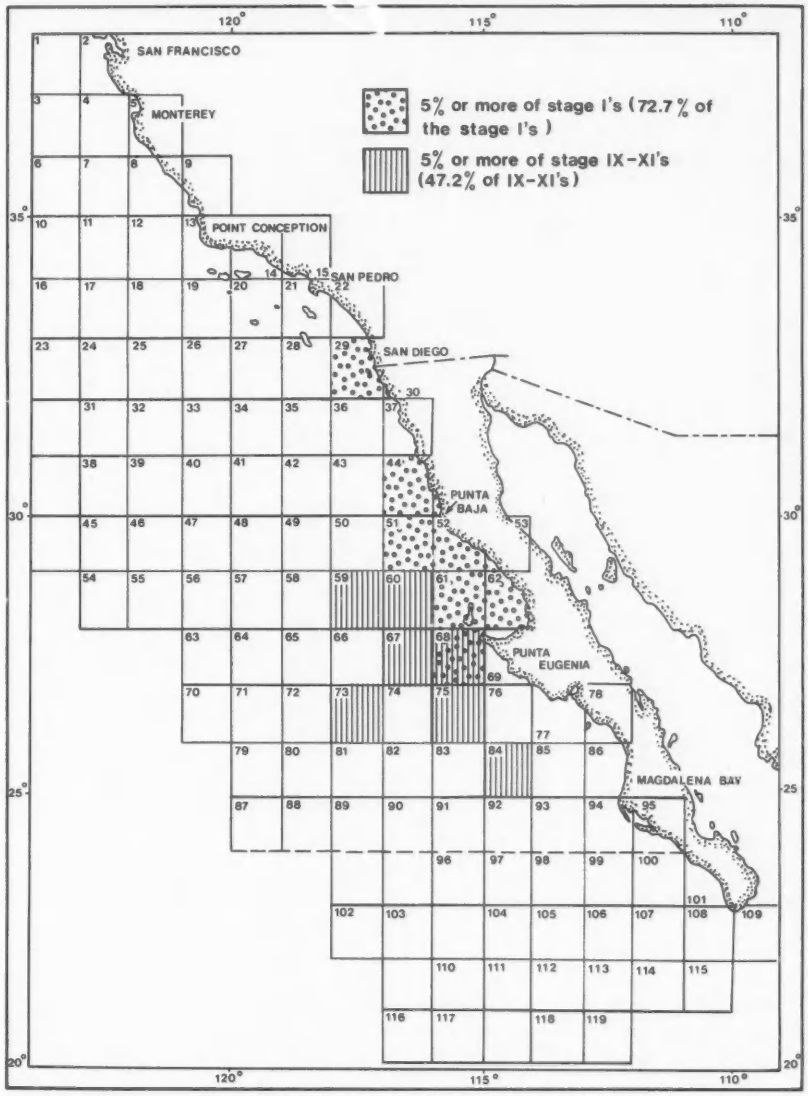


FIG. 3. Distribution of concentrations of both stage I and stage IX–XI *P. interruptus* phyllosome larvae in the California Current during 1949–55 inclusive (CalCOFI data from Johnson 1960a).

(1979) concluded, following a review, that "... no generally accepted explanation emerges from the data." They suggested that recruitment is either from down stream or via the "Johnson (1960b) model" described for *P. interruptus* (i.e. recruitment is due to the entrainment of larvae by nearshore gyres and eddies).

The best documented recruitment system for lobsters in general, and panulirids in particular, was summarized by Phillips (1981) for *P. cygnus* off western Australia. Here, workers (Chittleborough and Thomas 1969; Ritz 1972a, 1972b; Phillips et al. 1978; Rimmer and Phillips 1979; Phillips et al. 1979; Rimmer 1980) coupled larval behavior with physical oceanography to hypothesize a larval recruitment mechanism. The model includes ontogenetic changes in larval behavior in regard to diurnal vertical migration in relation to wind-generated Ekman transport and seasonally varying oceanic currents. Phyllosomes are interpreted to be transported hundreds of kilometres offshore and back again as recruits.

## Discussion

Johnson, in his final publication on the ecology of *P. interruptus* larvae (Johnson and Brinton 1963), suggested that the answer to the mechanism of larval recruitment "... will most likely be found to include some aspects of water movements correlated with the behavior and life history of the animals." Australian researchers (see previous section), after combining laboratory and field studies over a period of years, found sup-

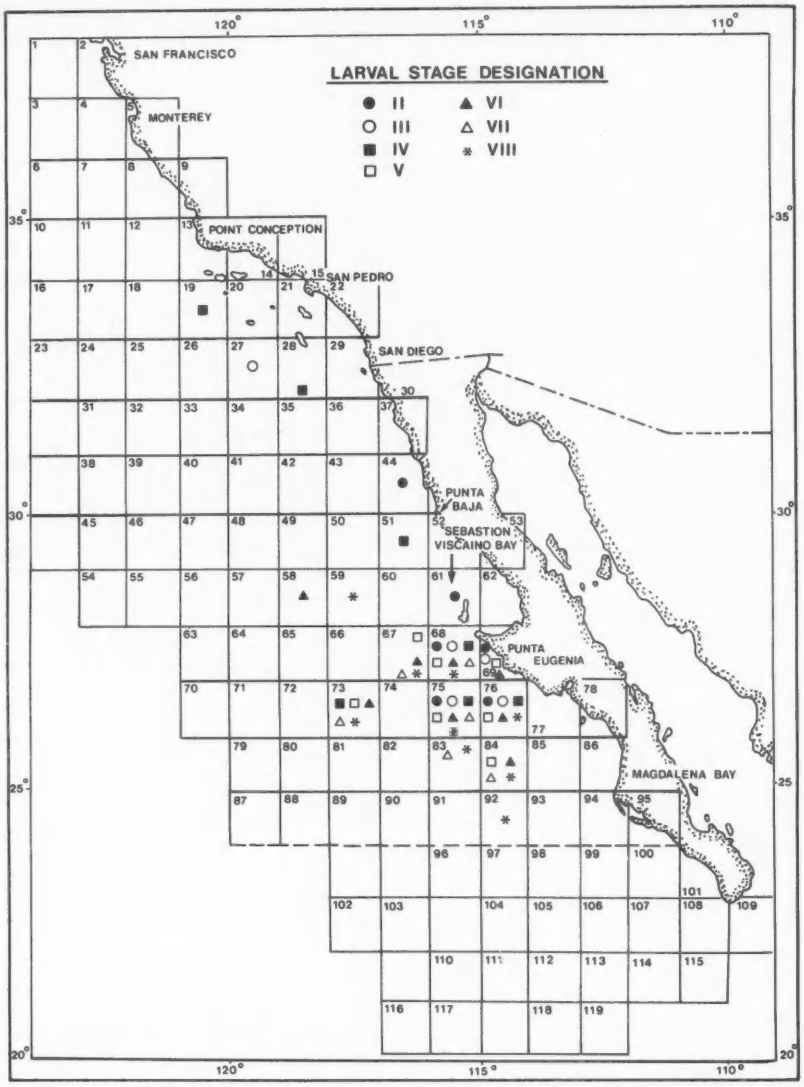


FIG. 4. Distribution of concentrations of *P. interruptus* larvae (stages II–VIII) in the California Current during 1949–55 inclusive (CalCOFI data from Johnson 1960a).

port for this hypothesis for the congeneric *P. cygnus*. The oceanographic systems found off western Australia and California differ. It is likely then that the larval retention mechanism and recruitment process differ as well.

A number of factors tend to refute the suggested similarity between *P. cygnus* and *P. interruptus* larval retention and recruitment mechanisms (Phillips 1986). First, although overall *P. interruptus* distribution is broad, the bulk of the larvae are concentrated relatively near shore (Fig. 1). Second, there is little relationship between patterns of both Ekman wind drift strength during critical seasons (summer and fall) and patterns of larval concentrations (Table 1). For example, larvae and adults were rare from Cape Mendocino to Pt. Conception and abundant from Punta Baja south; Ekman wind drift was strong to moderate and moderate, respectively. Where wind drift was weak, Pt. Conception to Punta Baja, larval abundances were low, a marked difference from the major finfish taxa (Parrish et al. 1981). Third, *P. cygnus* egg-bearing lobsters move offshore and egg-hatch whereas *P. interruptus* egg bearers move onshore. This offshore movement by *P. cygnus* females was interpreted as a mechanism to enhance larval offshore movement via Ekman wind drift.

Below, an attempt will be made to work the available knowledge into a retention and recruitment mechanism for *P. interruptus* phyllosomes. The following assumptions will be employed: first, the phyllosome concentrations (Fig. 1, 3, and 4) are the major source for puerulus recruits to the fishery nursery grounds (Engle 1979); and second, the larvae exhibit a diurnal vertical migration (near the surface during the dark period; at depth during the light period) and thus are not commonly found

solely in either deep water (Lindberg 1955; Johnson 1956) or in the neuston.

There was an overall lack of midstage phyllosome concentrations between Pt. Conception and Punta Eugenia, the location of the California spiny lobster fishery. Of particular interest was the meagre concentrations in the Southern California Bight and in particular the SCE. The latter was first hypothesized as a lobster larval retainer by Johnson (1960b). This concept was later supported by Owen (1980) and for other species by Hewitt (1981). However, Johnson and Brinton (1963) correctly concluded that the rate of direction of surface flow of the California Current would not retain a packet of water the 8 mo required to permit metamorphosis to the puerulus stage.

What then are the mechanisms for both phyllosome retention and obvious northward transport of either larvae or pueruli? The concentrations of midstages to the south of stage I concentrations preclude a major role for Ekman transport in larval advection. Similarly, this same stage differential in geographic location suggests that the zone of impingement of negative wind stress curl at Punta Eugenia plays less than a minor role in larval retention. However, not coincidentally, the concentrations of both mid- and late-stage phyllosomes are exactly located in the field of the mesoscale, perenially occurring, but semipermanent gyre (Hewitt 1981; Parrish et al. 1981). The gyre is spawned in the fall and disintegrates in the spring with the onset of strong Ekman transport (Parrish et al. 1981). The gyre longevity is approximately equal to that of the phyllosome life history (see Fig. 2).

Thus, it appears that the bulk of stage I phyllosomes are rapidly transported southward via the California Current. The distance from the center of stage I abundance (approximately degree-square 51, Fig. 3) to the center of stage II abundance (approximately degree-square 68, Fig. 4) is about 300 km. The abundance peaks are approximately 13 d apart (Fig. 2), which would require a transport of approximately 23 km·d$^{-1}$. California Current southward transport ranges from 6 cm·s$^{-1}$ (Winant and Bratokovich 1981) to 40 cm·s$^{-1}$ (Bernstein et al. 1977), sufficient at the upper range to perform the task. The suggested rapid southward transport would preclude the early-stage larvae spending much time, if any, in the Davidson Current.

The phyllosomes are retained for approximately 5 mo (to about February) in the gyre. Concentrations of stage VIII larvae occur at latitude 24°N, the most southerly larval concentration. With the onset of gyre decay the late stages are transported northeastward to about 29°N (Fig. 3) during March and April. This would suggest that these stages occur in the counterflowing Davidson Current, which in late winter is nearer the surface than during summer (Johnson 1960b).

Late-stage phyllosome concentrations (March–April) were yet a considerable distance seaward (Fig. 3) from both adult concentrations, as judged by the location of the fishery, and the nearshore nursery grounds (Engle 1979). Phillips et al. (1978) noted that *P. cygnus* late-stage phyllosome were even further from onshore nursery grounds; of the 1169 late stages captured, 9 only were over the continental shelf. Equal numbers of pueruli were captured both on and off the shelf, suggesting that metamorphosis occurs beyond the shelf. Phillips (1981) concluded that the role of the puerulus, being both a strong and directional swimmer (Phillips and Olsen 1975), is to swim the 40-km shelf to the nursery grounds. Phillips et al. (1978) found offshore *P. cygnus* pueruli at various depths, but captured a number at 90 m; they suggested that significant numbers may

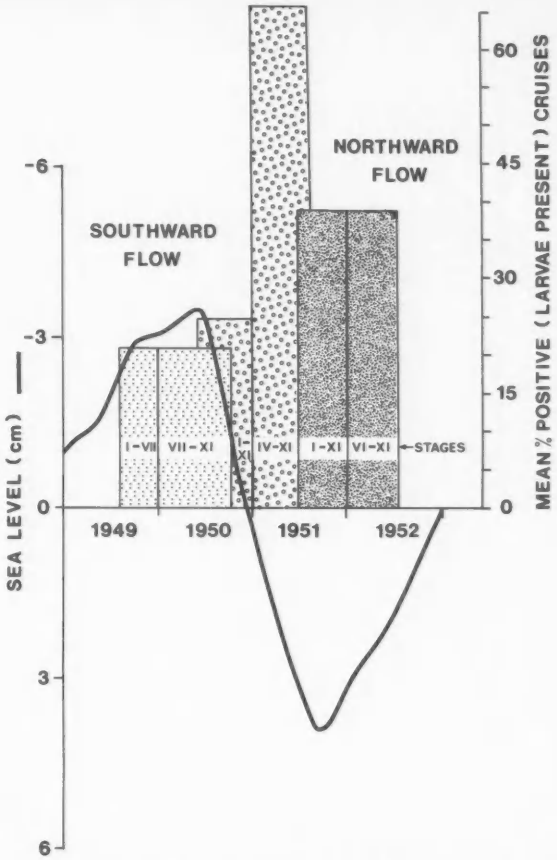


FIG. 5. Percent "positive" cruises (those cruises that captured *P. interruptus* phyllosome larvae; see Table 2) on the CalCOFI grid during 1949–52 inclusive compared with the steric height anomaly. Larval stages captured per temporal period are given.

even be deeper.

Serfling and Ford (1975) suggested that *P. interruptus* pueruli likewise had evolved specifically for recruitment, but at what depth is not known. The few pueruli identified from CalCOFI collections led Johnson (1960b) to conclude that they are a benthic form. Serfling and Ford (1975) disagreed; they presented a convincing argument that the puerulus morphology and behavior suggest a pelagic distribution. Based on nearshore collections only, they further suggested an upper water, and possibly even a neustonic, distribution for the pueruli. This may be correct nearshore, but is unlikely the case offshore, based on both the few captured by CalCOFI in vertical tows from 140 m (Johnson 1956) and prevailing oceanographic currents. Metamorphosis likely occurs about April–May offshore (compare Fig. 2 and 3), a period and location of strong, offshore Ekman transport (Table 1). If the pueruli were at the surface, they would be rapidly transported offshore. If they were somewhat deeper they would likely be transported southward, in spite of a calculated swimming speed of 8 cm·s$^{-1}$ (Serfling and Ford 1975). If they were below the California Current the counterflowing Davidson Current would transport them northwestward. Shoreward movement is either

TABLE 2. Number of cruises[a] (CalCOFI) per lobster larval year class (i.e. July–June inclusive), percentage positive (+) cruises per larval stage year class, and months of capture per stage for the year classes 1949, 1950, and 1951.

| | 1949–50 | | | | 1950–51 | | | | 1951–52 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Larval stage | No. "+" cruises | % "+" cruises | Mean % "+" cruises | Capture months | No. "+" cruises | % "+" cruises | Mean % "+" cruises | Capture months | No. "+" cruises | % "+" cruises | Mean % "+" cruises | Capture months |
| I | 3 | 30 | | Aug.–Oct. | 3 | 30 | | June, July, Sept. | 4 | 33.3 | | July–Oct. |
| II | 3 | 30 | | Aug.–Oct. | 1 | 10 | | Sept. | 4 | 33.3 | | Aug., Nov. |
| III | 3 | 30 | | Aug.–Oct. | 2 | 20 | 25.0 | Sept., Nov. | 5 | 41.7 | | Aug.–Dec. |
| IV | 3 | 30 | | Sept., Nov. | 3 | 30 | | Sept., Nov., Jan. | 5 | 41.7 | | Aug.–Dec. |
| V | 3 | 30 | | Sept., Nov. | 3 | 30 | | Sept., Nov., Jan. | 5 | 41.7 | | Aug.–Dec. |
| | | | 21.0 | | | | | | | | 37.9 | |
| VI | 2 | 20 | | | | | | | | | | |
| VII | 3 | 30 | | Oct., Nov. | 3 | 30 | | Sept., Nov., Feb. | 6 | 50.0 | | Aug.–Jan., Mar. |
| | | | | Oct., Nov., May | 5 | 50 | | Sept., Nov., Jan.–Mar. | 5 | 41.7 | | Sept.–Feb. |
| VIII | 0 | 0 | | | 7 | 70 | | Nov., Jan.–May | 4 | 33.3 | | Nov., Dec., Feb., May |
| | | | | | | | 66.6 | | | | | |
| IX | 2 | 20 | | Apr., July | 8 | 80 | | Nov., Jan.–June, Aug. | 7 | 58.3 | | Oct.–May |
| X | 0 | 0 | | | 5 | 50 | | Feb.–July | 5 | 41.7 | | Dec., Jan., Mar.–May |
| XI | 1 | 10 | | Nov. | 8 | 80 | | Jan.–Aug. | 6 | 50 | | Dec., Jan., Mar.–July |

[a]Number of cruises during the 1949 and 1950 year classes was 10 and during the 1951 year class was 12.

by swimming or a combination of swimming and physical transport by phenomenon such as internal waves (Shanks 1983).

Given the location of the above described larval retention system and the horizontal distribution of late-stage larval concentrations (Fig. 3), it is not surprising that the Mexican *P. interruptus* annual catch is seven times greater than that in the Southern California Bight (Engle 1979). Serfling and Ford (1975) suggested that pueruli captured onshore in the Bight (degree-square 29, Fig. 3) originated from late-stage phyllosomes maintained either close to shore or in eddies of the southern California Channel Islands. The average annual late-stage distributional data do not support this hypothesis (Fig. 3 and Johnson 1960b). An alternative source of postlarval recruits is from Mexican waters via the Davidson Current. Whether the pueruli would be transported from about 28 to 34°N without molting to the benthic stage is not known.

Another mechanism that could generate episodic, interannual pulses of larval recruitment to the northern portion of the range is the influence of ENSO events on the California Current described by Bernal (1981). Chelton et al. (1982), and Sinclair et al. (1985). During periods of weak southward or even northward flow of the California Current (i.e. during El Niño events), lobster larvae originating in the north would have a greater tendency to be retained locally. Also, a portion of the larger concentrations off central Baja California could be transported to the Southern California Bight. Unfortunately, the lobster fishery is too ill-defined and landings too inaccurate to use correlations between episodes of northward transport and time-lagged yield peaks to test this hypothesis.

Furthermore, Johnson (1960a, 1960b) did not present a complete time series of larval frequencies which could have been employed to test this hypothesis. He did, however, list all cruises (1949–56) and recorded whether each were successful (positive) or not (negative) in capturing phyllosomes (for a rarely distributed species such as *P. interruptus* larvae, this can be a measure of abundance). These data are used to evaluate, in a quantitative sense, the influence of the ENSO events on larval distribution. A major ENSO event occurred between 1949 and 1953. Steric height for 1949–53 was plotted against positive or negative cruises (Fig. 5). From 1949 to 1950 was a period of low steric height, hence a stronger than average southward flow. The mean percent of positive cruises during this period was 21.0 (Table 2). The period 1951–53 was one of weak southward flow, possibly even net northward flow. The mean percent of positive cruises between July and December was 25.0; the steric height during this period changed from −3 cm to 0. The steric height rose markedly, from 0 to +3, during January to June (1951) inclusive; the percent of positive cruises increased to 66.6. The same phenomena existed from July 1951 to June 1952 when the mean percent of positive cruises was 37.9. Not only did the El Niño waters tend to enhance larval recruits in the Southern California Bight, but the warmer waters appeared to increase larval molt frequency. For example, during late 1949 the most advanced larval stage recorded was VII; during late 1950 and 1951 the most advanced larval stage observed was XI (Fig. 5).

Further evidence in support of this hypothesis was provided by Johnson (1960a) in response to questions at the 1957 CalCOFI meeting. Hence, he included some raw, untreated larval distribution data for July 1957, the beginning of an El Niño event (Chelton et al. 1982). To support my hypothesis, larval abundance should have increased in the Southern Cali-

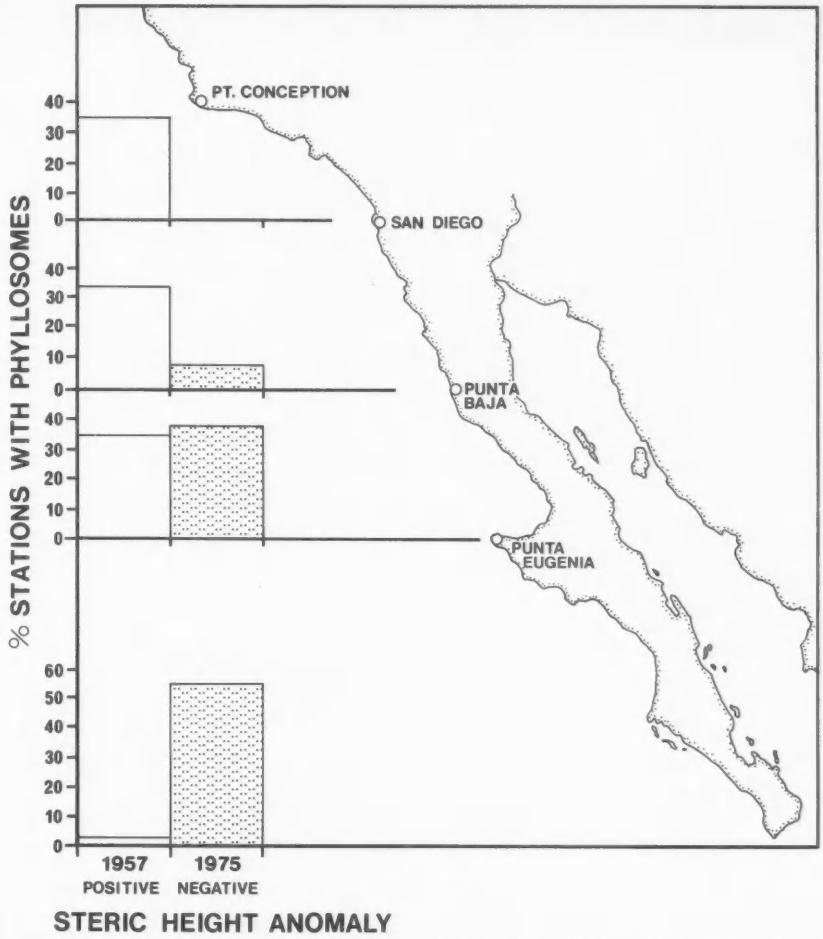


FIG. 6. Percentage of the "positive" CalCOFI stations sampled (where *P. interruptus* phyllosomes captured) for each of four geographic areas (Pt. Conception to San Diego, San Diego to Punta Baja, Punta Baja to Punta Eugenia, and Punta Eugenia south) during periods of positive (July 1957) and negative (October 1975) steric height anomalies.

fornia Bight. Johnson (1960a; and see Fig. 6) claimed that there was an unusually large number of early-stage larvae in the area, and in particular stage I abundance was "... far above average ...." Note that larval concentrations were as high in the Southern California Bight as off Punta Baja and Punta Eugenia. Few larvae were observed south of Punta Eugenia (Fig. 6). Some unpublished data (given to me by the late Dr. M. Johnson) from CalCOFI Cruise 7510 (October 1975), a period of low steric height and strong equatorward water flow, are also presented (Fig. 6). The larvae were definitely distributed in the south, and although 53 stations were occupied north of approximately 30°N, none were positive. Further support for the importance of El Niño currents on larval distribution is the extreme southerly distribution of larvae in November 1950. As noted earlier, nearly all the larvae taken south of 24°N were taken on this single cruise during a period of strong equatorward water flow.

Johnson's model (Johnson and Brinton 1963) of phyllosome larval retention within the adult along-shore range by gyres has been supported in this synthesis. However, there was little evidence to support a major role for the SCE. Most often the lobster larvae are swept out of the Southern California Bight to Baja California waters. It is suggested that during these years, if recruitment occurs, it is via pueruli transported northwestward on the Davidson Current. The interannual ENSO events tend to be characterized by warmer, and less equatorward flowing water. Evidence is given to support an hypothesis that these events could be the major source of lobsters to the Southern California Bight nursery grounds.

Lindberg (1955) speculated that the major source of lobster recruits to the Southern California Bight fishery originated from Mexican waters (this appeared to be based on the size of the respective fisheries). He then reasoned that the lobster egg production in Bight waters was of little consequence to this area's future fishery recruitment. A recommendation followed to reduce the minimium legal carapace size of lobsters in southern California waters to well below the size at first maturity. If the above recruitment scenario is correct, Lindberg's (1955) recommendation cannot be supported. Furthermore, management of the *P. interruptus* resource should be carried out bilat-

erally, between the two fishing states, for it is obvious that it is a transboundary stock.

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## References

ALLAN, W. E. 1945. Vernal distribution of marine plankton diatoms offshore in southern California in 1940. Bull. Scripps Inst. Oceanogr. Univ. Calif. 5: 335–370.

ALLEN, B. M. 1916. Notes on the spiny lobster (*Panulirus interruptus*) of the California coast. Univ. Calif. Publ. Zool. 16: 139–152.

AUSTIN, H. M. 1972. Notes on the distribution of phyllosoma of the spiny lobster, *Panulirus* spp. in the Gulf of Mexico. Proc. Natl. Shellfish Assoc. 62: 23–30.

BERNAL, P. A. 1981. A review of the low-frequency response of the pelagic ecosystem in the California Current. Calif. Coop. Oceanic Fish. Invest. Rep. 22: 49–62.

BERNSTEIN, R. L., L. BREAKER, AND R. WHRITNER. 1977. California Current eddy formation: ship air and satellite results. Science (Wash., DC) 195: 353–359.

CHELTON, D. B., P. A. BERNAL, AND J. A. MCGOWAN. 1982. Large-scale interannual physical and biological interaction in the California current. Mar. Res. 40: 1095–1125.

CHITTLEBOROUGH, R. G., AND L. R. THOMAS. 1969. Larval ecology of the Western Australian marine crayfish, with notes upon other panulirid larvae from the eastern Indian Ocean. Aust. J. Mar. Freshwater Res. 20: 199–223.

CUNNINGHAM, J. T. 1892. Observations on the larvae of *Palinurus vulgaris*. Rep. 61st Meet. Br. Assoc. Adv. Sci. 867 p.

DEXTER, D. M. 1972. Molting and growth in laboratory reared phyllosomes of the California spiny lobster (*Panulirus interruptus*). Calif. Fish. Game 58: 107–115.

DUFFY, J. M. 1973. Status of the California spiny lobster resource. Mar. Res. Tech. Rep. 10: 30 p.

ENGLE, J. 1979. Ecology and growth of juvenile California spiny lobsters (*Panulirus interruptus* Randall). Ph.D. dissertation, University of Southern California, Los Angeles, CA. 298 p.

GURNEY, R. 1936. Larvae of decapod crustaceans Part III: Phyllosome discovery. Report 12: 400–440.

HARADA, E. 1957. Ecological observations on the Japanese spiny lobsters (*Panulirus japonicus* von Seibald) in its larval and adult life. Publ. Seto. Mar. Biol. Lab. 6: 91–120.

HEWITT, R. 1981. Eddies and speciation in the California current. Calif. Coop. Oceanic Fish. Invest. Rep. 22: 96–98.

INGLE, R. M., B. ELDRED, H. W. SIMS, AND B. A. ELDRED. 1963. On the possible Caribbean origin of Florida's spiny lobster populations. Fla. Board Conserv. Mar. Lab. Tech. Ser. 40: 1–12.

JOHNSON, M. W. 1954. Plankton of the North Marshall Islands, Bikini and nearby atolls. Part 2. Oceanography (biological). U.S. Geol. Surv. Prof. Pap. 260F: 301–314.

1956. The larval development of the California spiny lobster, *Panulirus interruptus* (Randall) with notes on *Panulirus gracilus* Streets. Proc. Calif. Acad. Sci. Fourth Ser. 29: 1–19.

1960a. The offshore drift of larvae of the California spiny lobster, *Panulirus interruptus*. Calif. Coop. Oceanic. Fish. Invest. Rep. 7: 147–161.

1960b. Production and distribution of larvae of the spiny lobster *Panulirus interruptus* (Randall) with records on *P. gracilis* (Streets). Bull. Scripps Inst. Oceanogr. Univ. Calif. 7: 413–446.

JOHNSON, M. W., AND E. BRINTON. 1963. Biological species, water masses and currents, p. 381–414. *In* M. W. Hill [ed.] The sea, ideas and observations on progress in the study of the seas. John Wiley & Sons, New York, NY. 554 p.

LEWIS, J. B. 1951. The phyllosome larvae of the spiny lobster (*Panulirus argus*). Bull. Mar. Sci. Gulf Caribb. 1: 89–103.

LINDBERG, R. G. 1955. Growth, population dynamics and field behavior in the spiny lobster, *Panulirus interruptus* (Randall). Univ. Calif. Publ. Zool. 59: 157–248.

LITTLE, E. J. 1977. Observations on the recruitment of postlarval spiny lobsters (*Panulirus argus*) to the south Florida coast. Fla. Mar. Res. Publ. 29: 33 p.

LYONS, W. G. 1980. The postlarval stage of scyllaridean lobsters. Fisheries 5: 47–49.

MCGOWAN, J. A., AND E. BRINTON. 1985. Martin W. Johnson. Bull. Mar. Sci. 37: 407–410.

MENZIES, R. A., AND J. M. KERRIGAN. 1979. Implications of spiny lobster recruitment patterns of the Caribbean — a biochemical genetic approach. Proc. Gulf Caribb. Fish. Inst. 31: 164–178.

MOOERS, C. N. K., AND A. R. ROBINSON. 1984. Turbulent jets and eddies in the California Current and inferred cross shore transports. Science (Wash., DC) 223: 51–53.

OWEN, R. W. 1980. Eddies of the California Current system: physical and ecological characteristics, p. 237–263. *In* D. Power [ed.] The California Islands. Proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, CA. 787 p.

PARRISH, R. H., C. S. NELSON, AND A. BAKUN. 1981. Transport mechanisms and reproductive success of fishes in the California Current. Biol. Oceanogr. 1: 175–203.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster, p. 11–39. *In* M. Barnes [ed.] Oceanogr. Mar. Biol. Annu. Rev. 19.

1986. Prediction of commercial catches of the western rock lobster *Panulirus cygnus*. Can. J. Fish. Aquat. Sci. 43: 2126–2130.

PHILLIPS, B. F., P. A. BROWN, D. W. RIMMER, AND D. D. REID. 1979. Distribution and dispersal of the phyllosoma larvae of the western rock lobster (*Panulirus cygnus*) in the southeastern Indian Ocean. Aust. J. Mar. Freshwater Res. 30: 773–783.

PHILLIPS, B. F., AND L. OLSEN. 1975. Swimming behavior of the puerulus stage of the western rock lobster. Aust. J. Mar. Freshwater Res. 26: 415–417.

PHILLIPS, B. F., D. W. RIMMER, AND D. D. REID. 1978. Ecological investigations of the late stage phyllosoma and puerulus larvae of the western rock lobster *Panulirus longipes cygnus*. Mar. Biol. 45: 347–357.

REID, J. L. 1982. An oceanographic perspective. Calif. Coop. Oceanic Fish. Invest. Rep. 23: 39–42.

RIMMER, D. W. 1980. Spatial and temporal distribution of early stage phyllosoma of western rock lobster (*Panulirus cygnus*). Aust. J. Mar. Freshwater Res. 31: 485–497.

RIMMER, D. W., AND B. F. PHILLIPS. 1979. Diurnal migration and vertical distribution of phyllosoma larval of the western rock lobster *Panulirus cygnus*. Mar. Biol. 54: 109–124.

RITZ, D. A. 1972a. Behavioral response to light of the newly hatched phyllosoma larvae of *Panulirus longipes cygnus* George (Crustacea: Decapoda: Palinuridae). J. Exp. Mar. Biol. Ecol. 10: 105–114.

1972b. Factors affecting the distribution of rock lobster larvae (*Panulirus longipes cygnus*) with reference to variability of plankton-net catches. Mar. Biol. 134: 309–317.

RUSSEL, F. S. 1923–25. The vertical distribution of marine macroplankton. Biol. Assoc. U.K. 13: 769–809.

SERFLING, S. A., AND R. F. FORD. 1975. Ecological studies of the puerulus larval stages of the California spiny lobster, *Panulirus interruptus*. Fish. Bull. 73: 360–377.

SHANKS, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13: 311–315.

SIMS, H. W. 1966. The Florida spiny lobster. Fla. Board Conserv. Mar. Res. Lab. Southw. Fish. Leafl. 7: 1–15.

SIMS, H. W., AND R. M. INGLE. 1966. Caribbean recruitment of Florida's spiny lobster populations. Q. J. Fla. Acad. Sci. 29: 207–242.

SINCLAIR, M., M. J. TREMBLAY, AND P. BERNAL. 1985. El Niño events and variability in a Pacific mackerel (*Scomber japonicus*) survival index: support for Hjort's second hypothesis. Can. J. Fish. Aquat. Sci. 42: 602–608.

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING. 1942. The oceans. New York Prentice-Hall Inc., New York, NY. 1087 p.

WINANT, C. D., AND A. W. BRATOKOVICH. 1981. Temperature and currents on the southern California shelf: a description of the variability. Phys. Oceanogr. 11: 71–86.

# The Pelagic Phase of Spiny Lobster Development

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A reappraisal of the pelagic phase of development in palinurid lobsters, in conjunction with recent oceanographic data, shows that the ontogenetic changes in the vertical migratory behaviour of phyllosoma larvae operate as a biological strategy to effect larval recruitment. Wind-driven surface currents can transport the larvae in the opposite direction to the general circulation of the upper 300 m water layer. Ocean circulation charts are unreliable indicators of likely paths of larval transport because of their gross scale, lack of seasonal information, and the absence of indications of wind-driven surface currents. The majority of larvae are transported beyond the continental shelf to areas greater than 100 km offshore. This appears to be the principal source of larval recruitment to benthic populations, although some local recruitment from coastal areas may occur. Larval transport between populations of *Jasus* sp. in the Southern Ocean appears likely but is unconfirmed. For some insular populations this may be the sole, or major, source of recruitment. Delayed development of phyllosomata, or of pueruli, may account for year-round settlement in some species. Salinity changes are implicated as a factor stimulating metamorphosis from the final phyllosoma larval stage. The pelagic phase is completed by the nektonic, puerulus stage which swims (possibly directionally) across the continental shelf before settling and metamorphosing into the benthic stage.

Un réexamen de la phase pélagique de développement des langoustes de la famille des palinuridés, à la lumière de données océanographiques récemment obtenues, montre que les changements ontogéniques dans le comportement de migration verticale des larves phyllosomes constituent une stratégie biologique servant au recrutement des larves. Les courants superficiels dus au vent peuvent transporter les larves dans une direction opposée à la circulation générale dans la couche supérieure de 300 m. Les cartes de la circulation océanique constituent des indicateurs peu fiables de la direction vraisemblable du transport des larves à cause de leur grande échelle, de l'absence d'information à caractère saisonnier et de l'absence d'indications sur les courants superficiels dus au vent. La majorité des larves sont transportées, au-delà du plateau continental, vers des zones pouvant se situer à plus de 100 km des côtes. Ce phénomène semble être la principale source de recrutement des larves dans les populations benthiques, bien qu'il puisse y avoir un peu de recrutement local à partir des zones côtières. Le transport des larves entre populations de *Jasus* sp. dans les mers du sud semble vraisemblable, mais n'est pas confirmé. Pour certaines populations insulaires, il peut constituer l'unique ou la principale source de recrutement. Le retard de développement des phyllosomes ou des puerulus peut expliquer que certaines espèces s'installent sur le fond tout au long de l'année. Les changements de la salinité constituent un facteur qui stimule la métamorphose après le dernier stade larvaire phyllosome. La phase pélagique s'achève avec le stade nectonique puerulus pendant lequel l'animal nage (peut-être dans une direction donnée) d'un côté à l'autre de la plate-forme continentale avant de s'installer sur le fond et de connaître la métamorphose du stade benthique.

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The Palinuridae (spiny or rock lobsters), together with the Scyllaridae (slipper lobsters) and the Synaxidae (coral lobsters), are widespread and occur in most of the temperate and tropical regions of the world (Kanciruk 1980).

Part of the reason for the evolutionary success of these animals is the development of unique stages in the pelagic portion of their life cycle (Phillips et al. 1980). All develop initially through a series of zoea stages of a characteristic, planktonic larva called the phyllosoma (New Latin from Greek *phyll-* + *-soma*, plural *-somata* (see Webster's Dictionary 1981)). The dorso-ventrally flattened, leaflike body of the phyllosoma, coupled with its long duration, apparently results in an ideal form for dispersal and phyllosomata are well known as larvae characteristic of the open ocean (Phillips and Sastry 1980). This widespread dispersal of phyllosomata has the potential for effecting gene flow between populations of distant adults.

In addition to the phyllosoma larval stages, a nektonic stage occurs, forming a transitional link between the planktonic and benthic phases of the life cycle. This stage has been variously called a "puerulus", "post-larva", "natant", "nisto", "pseudibacus", or "reptant larva" (see Lyons 1970). Lyons (1980) correctly pointed out that "puerulus" normally is applied only to members of the Palinuridae; he suggested "post-larva" to designate the stage following the last phyllosoma larval stage

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of both the Palinuridae and Scyllaridae. This stage corresponds to the megalopa stage of the Brachyura, as its swimming is achieved by the now fully formed abdominal appendages (pleopods), not the thoracic appendages (pereiopods) as in the phyllosoma stages (Williamson 1982). The megalopa form of the Scyllaridae, the nisto, is much closer in appearance to its adult form than is the puerulus in the Palinuridae and it may lack the swimming ability of the puerulus (Latin *puerulus*, plural *-i*). Hence, the functional role of the post-larval stage in the two families may be different. Phillips and Sastry (1980) used the term "nisto" to distinguish this stage in scyllarids from the "puerulus" stage of palinurids; this distinction will be followed in this paper.

Studies of the larval transport of palinurid species have been mainly descriptive or speculative; hence, our knowledge of their dispersal and recruitment mechanisms is poor (Phillips and Sastry 1980). In only a few species have all the developmental stages been described. For fewer still are there sufficient data on ocean current systems to support a description of possible dispersal and larval recruitment pathways. Relevant taxonomic or ecological studies of the past 15 yr include work on the phyllosoma stages and puerulus of *Panulirus cygnus* George (Phillips 1972, 1975a, 1975b; Phillips and Hall 1978; Rimmer and Phillips 1979; Rimmer 1980; Phillips et al. 1978; Braine et al. 1979; Phillips 1981), the pueruli of *Panuliris interruptus* (Randall) (Parker 1972; Serfling and Ford 1975) and *Panulirus argus* (Latrielle) (Calinski and Lyons 1983), the phyllosomata of *Panulirus gracilis* (Streets) (Baez 1983), the pueruli of *Panuliris marginatus* (Quoy and Gaimard) (MacDonald 1986), the phyllosomata of *Panulirus longipes femoristriga* (von Martens) (McWilliam and Phillips 1983; Phillips and McWilliam 1986), the phyllosoma stages of *Jasus frontalis* (H. Milne Edwards) (Baez 1973), the phyllosoma stages and puerulus of *Jasus edwardsii* (Hutton) (Lesser 1974, 1978; Booth 1979; Booth and Tarring 1982), the phyllosoma stages (McWilliam and Phillips 1986) and puerulus of *Jasus verreauxi* (H. Milne Edwards) (Booth 1986), the phyllosoma stages of *Jasus novaehollandiae* Holthuis (Lewis 1977; McWilliam and Phillips 1986), the puerulus of *Jasus lalandii* (H. Milne Edwards) (Pollock 1973; Pollock and Goosen 1983), the final phyllosoma of *Jasus tristani* Holthuis (Miller 1985), and the phyllosomata and pueruli of *Scyllarus bicuspidatus* (De Man) (Phillips et al. 1981; McWilliam and Phillips 1983).

The study of oceanic circulations has advanced significantly since 1972 with the use of modern techniques including satellite-tracked buoys, satellite photography, and computer simulation. This has greatly improved our understanding of oceanic currents, particularly in providing synoptic pictures of the currents of the oceans (e.g. Richards and Goulet 1977; Lai and Richardson 1977; Lutjeharms and Heydorn 1981a, 1981b; Lutjeharms and Valentine 1981; Owen 1981) and meso-scale eddies in western (Nilsson and Cresswell 1981; Jenks et al. 1982; Grundlingh 1983) and eastern (Cresswell and Golding 1980; Owen 1980; Godfrey and Ridgway 1985) boundary currents.

It is not our intention to review all of the data which are now available on the pelagic stages and the currents in which they occur. Rather, we propose to examine three questions which are fundamental to our understanding of larval transport and/or recruitment to the benthic stock at the end of the pelagic cycle.

(1) Are phyllosomata simply at the mercy of ocean currents, or do they have well-developed behavioural responses to environmental stimuli which allow them to use currents to return to the adult habitat? This is addressed under the section Biological Strategy or Random Larval Recruitment?

(2) What is the extent of larval transport? This is addressed under the section Larval Transport Between *Jasus* Populations Around the Southern Ocean.

(3) What is the role of the puerulus stage? This is discussed under the section Role of the Puerulus in Recruitment to the Benthic Stock.

## Biological Strategy or Random Larval Recruitment?

The changing vertical migratory behaviour of the phyllosoma during its development operates as a biological strategy to effect larval recruitment.

### Vertical Migration and Larval Recruitment

Vertical migration patterns are integrated with larval transport. Although phyllosomata may be incapable of effective horizontal swimming, they are able to achieve vertical movement and, like most planktonic crustaceans (Raymont 1983), carry out vertical migrations.

Nevertheless, most of the early studies, and some recent models, of phyllosomata dispersal were based on the assumption that these larvae may be treated simply as floating objects transported by currents (e.g. *P. interruptus*, Johnson 1960a; *P. argus*, Ingle et al. 1963; Richards and Goulet 1977; *J. novaehollandiae*, Winstanley 1970; *P. interruptus* and *P. cygnus*, Jackson and Strathmann 1981; *P. cygnus*, B. V. Hamon, CSIRO Australia, pers. comm.). These studies ignore the effect of vertical migration on the transport of the larvae. In fact, Johnson and Brinton (1963) remarked that the phyllosoma larva "unlike drift bottles, may exercise some degree of modification of their distribution." These authors also suggested that some strategy was coupled with diurnal vertical migration behaviour to keep larvae within a region by alternative periods spent in currents flowing in different directions or at different speeds.

The importance of vertical migration in larval transport is exemplified by the larval behaviour of *P. cygnus* (Rimmer and Phillips 1979). The vertical migration behaviour of early phyllosoma stages (I–III) of *P. cygnus* takes them to the surface. They are transported offshore into the southeastern Indian Ocean by the surface wind drift (Cresswell 1972) at about 5.25 $km \cdot d^{-1}$ (Rimmer and Phillips 1979; Phillips et al. 1979). This is in the opposite direction to the general circulation of the upper 300 m layer which flows east towards the coast of Western Australia at about 3.3 $km \cdot d^{-1}$ (Wyrtki 1962; Hamon 1965). In *P. cygnus*, mid- and late-stage (IV–IX) phyllosomata avoid the surface layer during most of the larval phase because of their increasing sensitivity to light (Rimmer and Phillips 1979). Because of this behaviour they become more subject to the subsurface circulation which returns them near to the coast of Western Australia (Phillips et al. 1979; Phillips 1981). A summary of the pelagic phase of *P. cygnus* is presented in Fig. 1.

The use of different vertical behaviour permits *S. bicuspidatus* to maintain a different dispersal and larval recruitment pattern to *P. cygnus* within the southeastern Indian Ocean (Phillips et al. 1981).

### Circulation Patterns

Ocean circulation charts cannot be used as reliable indicators

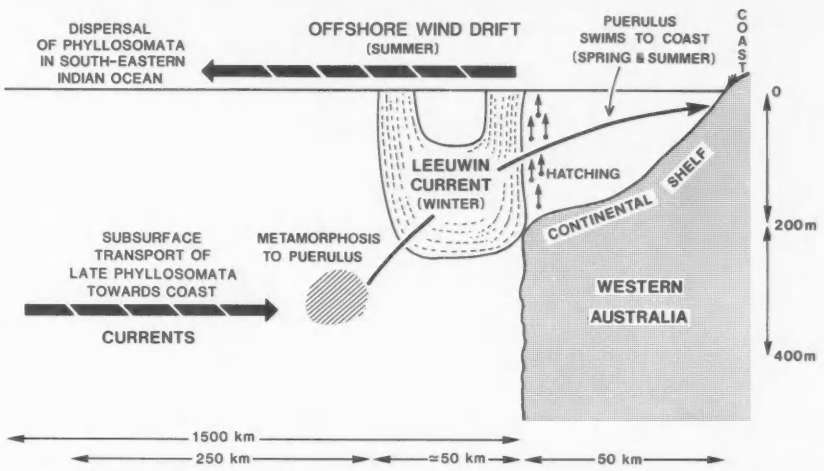


FIG. 1. Summary of the oceanic cycle of *Panulirus cygnus*. Early phyllosoma stages stay at day depths of 30–60 m, but concentrate near surface at night. Thus, they are exposed to the wind-driven surface layer and transported well offshore. Mid- and late stages avoid the surface layer during most of the lunar phase because of increasing sensitivity to light. Therefore, they are subject predominantly to the subsurface circulation which is an easterly flow towards the coast. After metamorphosis, the puerulus swims across the shelf and settles in inshore reef areas.

of the likely paths of larval transport. Details of the circulation of the oceans generally are not available on the scale required for satisfactory understanding of larval advection. This is a problem which arises particularly in relating larval advection to currents in the upper part of the water column. These currents are often variable and are vaguely known by returns of drift bottles and surface drogues. Different interpretations of the oceans' currents are depicted by different authors (e.g. Sverdrup et al. 1942; Defant 1961; McLellan 1965; Cutler and Swallow 1984). The large-scale circulations depicted by such representations are gross simplifications of the data which give no indication of complexity, or seasonal variations, of water movements on a smaller scale. Off Western Australia, in the scale of relevance for the larvae of *P. cygnus*, we know now that the circulation is very different from that depicted by Defant (1961) (see Fig. 2a). Even the circulation pattern depicted by Pearce and Cresswell (1985) (Fig. 2b) gives no hint of the eddy field of both anticlockwise and clockwise eddies which occur within the illustrated circulation pattern.

Few representations of ocean circulation patterns make any attempt to indicate wind-driven surface currents (e.g. Fig. 2a or 2b). Satellite-tracked buoys are providing data on some water movements. However, the design of these buoys imposes considerable limitations on the data obtained. For example, the drogue attached to the buoy is usually about 20 m below the surface and provides a measure of the water movement at that level. The phyllosomata, however, move vertically through the water column and may be subject to a range of circulation features in a single day. Thorson (1961) once dismissed this criticism with the argument that the movements of the upper 300 m of the water column are much the same throughout this depth range. But more recent hydrological investigations (e.g. Godfrey and Ridgway 1985) indicate that such homogeneity of flow is not necessarily the case. The drogues are normally set to avoid the major effects of surface currents generated by the wind, and it is these currents that at times seem to be very important in the transport of larvae (e.g. *P. cygnus*). In studies of wind-driven transport it must be borne in mind that because of Coriolis effects the net transport is not necessarily in the direction of the wind. For example, a wind parallel to the coast may generate an offshore current.

On the other hand, the extent or pattern of dispersal of phyllosomata can contribute to an understanding of water movements. The absence of described water movements in an area may be the result of inadequate data, lack of investigation, or because the flow is not readily detected by the usual physical oceanographic methods. The existence of the subtropical countercurrent extending from the western boundary of the Pacific to the region of the Hawaiian Islands was predicted from a theoretical study by Robinson (1969) but not confirmed until 1978 (Hasunuma and Yoshida 1978). The presence in waters off Hawaii of a few phyllosomata of *P. longipes femoristriga* and *Scyllarus demani* Holthuis, apparently transported from islands in the Western Pacific (Phillips and McWilliam 1986), offers additional confirmation. Similarly, the return Agulhas circulation, which may be the means of transport of larvae of *Palinurus delagoae* Barnard and *Palinurus gilchristi* Stebbing off Africa, has been described only recently (Heydorn 1978).

## Larval Wastage

Phyllosoma larvae are distributed widely in the oceans, and the presence of adults in an area is more likely to be affected by successful settlement and survival after settlement than by transport of the larvae. Earlier studies of Northern Hemisphere palinurid species have led to a long-held tenet that larval recruitment was effected only by phyllosomata that remained near the coast, and that offshore larval dispersal was tantamount to loss.

Johnson (1960a, 1960b, 1971) hypothesized that most, if not all, of the larvae of *Panuliris pencillatus* Oliver, *P. inflatus* Bouvier, *P. gracilis*, and *P. interruptus* found further than 100 km offshore represented a loss to the population. He suggested further that recruitment occurred from the larvae which

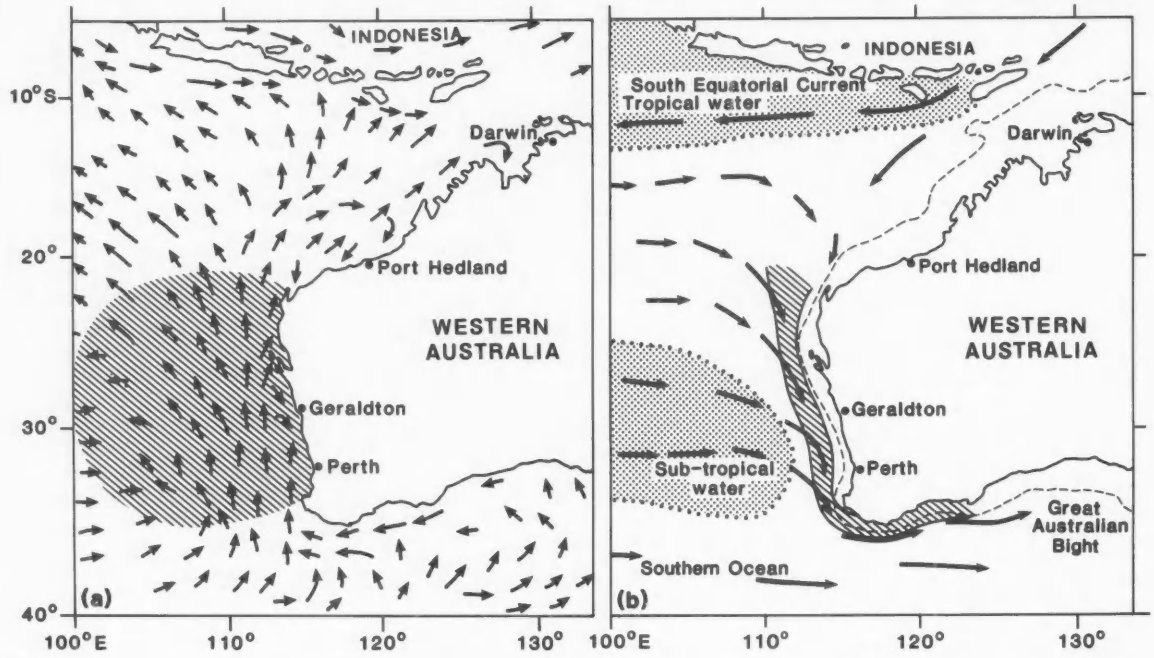


FIG. 2. (a) Oceanic sea-surface currents off Western Australia (after Defant 1961) superimposed on the known extent of the larval distribution of *Panulirus cygnus*, shown as a shaded area. (b) Schematic chart of the mean large scale circulation of the eastern Indian Ocean (after Pearce and Cresswell 1985). The edge of the continental shelf (broken line represents the 200-m isobath). The Leeuwin Current is the southward flow of warm, low-salinity water down the Western Australian shelfbreak.

were held in coastal eddies and gyres around islands and shallow areas less than 100 km offshore near the coast.

Johnson's hypothesis has been influential, but it hinges on the definition of the word "coastal." Serfling and Ford (1975) stated that both Johnson (1960b) and Chittleborough (1970) showed that large numbers of late-stage phyllosoma larvae remained well within the coastal areas in which the earlier larval stages occur. In fact, neither Johnson (1960b) nor Chittleborough (1970) reached this conclusion. Johnson (1960b) stated that stages IX, X, and XI (the final phyllosoma stage) of *P. interruptus* "maintained a distant offshore distribution." Chittleborough and Thomas (1969) concluded "from the sampling which has been carried out so far, it is evident that in late autumn and throughout winter the densities of [*P. cygnus*] larvae found within 100 miles of the coast are so low that larvae would need to come from a greater distance in order to maintain the population."

Similarly, Sastry (1983) generalised that "Phyllosoma larvae are retained within the continental shelf by hydrographical processes such as eddies and the direction of water movement at different depths." However, Phillips (1981) reported that most *P. cygnus* breeding adults are found on the outer portions of the continental shelf about 40–60 km from the coast and that during the long planktonic period, few, if any, phyllosomata remain in the waters on or near the continental shelf of Western Australia.

There is accumulating evidence from Southern Hemisphere studies that phyllosomata develop through most of their stages well offshore. Studies of *P. cygnus* (Chittleborough and Thomas 1969; Phillips et al. 1979; Phillips 1981), *J. edwardsii* (Lesser 1978; Booth 1980), *J. lalandii* (Lazarus 1967; Pollock and Goosen 1983), and *J. verreauxi* (Booth 1986) have all confirmed that the majority of mid- and late-stage phyllosomata of these species are dispersed well offshore and are virtually absent from the continental shelf and near coastal waters. Transport of the larvae over hundreds, or even thousands, of kilometres is indicated, with the larvae passing over, or through, a number of water masses before recruitment back to the benthic stock.

Evidence of a wide offshore dispersal of larvae does not imply that some recruitment could not occur from coastal areas and that the source might not vary from year to year. In fact, Johnson (1960b) felt that additional sampling for *P. interruptus* in shallow water was needed to measure the extent of larvae in these areas and their contribution to the population. Recruitment in *P. interruptus* may well be very different from that in *P. cygnus*. Off California, the continental shelf is narrow but a large number of islands and shallow banks are relatively close to shore, and the mixing of eddies associated with these features possibly helps to retain larvae in the area (Hewitt 1981).

## Distant Transport

It is known that some of the phyllosomata that do not return to the area of origin can metamorphose and settle in other areas. However, often their ensuing stages die as juveniles or fail to reproduce. Naturally, some random dispersal must be involved in larval transport processes. For example, the phyllosoma larvae of *P. cygnus* become widely distributed throughout the southeastern Indian Ocean, but are in greatest abundance

375–1030 km offshore, directly west of the centre of distribution of the adult population on the coast (Phillips et al. 1979). Dispersal from this area presumably includes random dispersal by ocean currents on a variety of scales.

The larvae that drift farthest from the coast where the adult stock resides are probably lost to the population, but the maximum distance offshore from which the larvae can return successfully is not known for any species. The larvae of *P. cygnus* were found in considerable numbers out to 1500 km offshore (the limit of the sampling) (Phillips et al. 1979), and larvae of *P. penicillatus* and *P. gracilis* have been found at distances of 3300–3700 km from their point of likely origin (Johnson 1974).

Berry (1974) has suggested that larval transport of *Panuliris homarus rubellus* Berry occurs between Madagascar and southeastern Africa, and larval transport of *P. argus* from the American continent to Abidjan, West Africa, has been recorded (Marchal 1968). Guerra and Gaudengio (1982) reported the presence of *J. lalandii* from South Africa on the Portugese coast. However, at least one attempt apparently has been made to introduce *J. lalandii* to Europe, and these specimens might have resulted from this source (G. Y. Conan, University of Moncton, Moncton, N.B., pers. comm.). These chance survivals of individuals do not significantly alter the larval recruitment and survival of the adult populations of these species, as, in most cases, only a very small proportion of the total number of larvae produced are needed to maintain the benthic population.

Other, more significant larval contributions probably do occur, but over shorter distances. Studies of *Panulirus ornatus* (Fabricius) in Torres Strait between Papua New Guinea and Australia (Phillips et al. 1983; Moore and MacFarlane 1984; Bell et al. 1986) have shown that the main breeding population occurs at the eastern end of the Gulf of Papua, in Papua New Guinea, although small numbers of breeding females have been found on the northeastern coast of Queensland, Australia. The breeding population in the eastern Gulf of Papua appears to supply the larvae producing the adult stocks in Papua New Guinea waters, in Torres Strait, and also along the northeastern coast of Queensland. The significant point is that, although the population in Torres Strait contributes to the breeding stock in the Gulf of Papua, the animals on the northeastern coast of Queensland apparently do not.

The adult distribution range of a species may be extended latitudinally by dispersal of a small proportion of its larvae. *Palinurus elephas* Fabricus is found in northwestern Europe (Tambs-Lyche 1958; Rae and Lamont 1963). The most northerly record of egg-bearing females is in the Inner Hebrides. However, the range of nonbreeding adults extends to northern Scotland, the Orkney and Shetland islands, and western Norway. The shortest route (from the most northerly breeding record) to the Norwegian coast is about 926 km, but it seems more likely that the Norwegian specimens were hatched in western Ireland, where ovigerous females are common, and that the larvae travelled at least 1480 km (Williamson 1967). Similarly, a few *P. longipes femoristriga* are found along the northern coast of New South Wales, Australia (George and Holthuis 1965), but no breeding populations are found in this area. It is believed that their southward dispersal is effected by larval transportation in the East Australian Current (McWilliam and Phillips 1983).

The occurrence of year-round settlement reported for some species does not refute the hypothesis that recruitment occurs from local populations. Year-round larval recruitment of the puerulus stage of *P. argus* in Florida (Little 1977) has been cited by Menzies (1981) to challenge the hypothesis that recruitment in *P. argus* occurs from Florida populations. The data for *P. cygnus* (Phillips and Hall 1978) showed that, although peak settlement occurs between September and January each year, some settlement can occur throughout the year. In the single breeding stock of *P. cygnus*, larval release occurs between November and March (Rimmer 1980). Delayed development of the larvae, or of the pueruli, is therefore clear in the case of *P. cygnus*, and it may also occur in *P. argus*, and could account for year-round settlement in that or other palinurid species.

### Dispersal Without Settlement or Death Soon After Settlement

In some cases the pueruli apparently fail to settle successfully or die as very young juveniles. Phyllosoma larvae of *S. demani* and *P. longipes femoristriga* are found near the coast of Hawaii (Phillips and McWilliam 1986) but adults have not been reported from the Hawaiian Islands. Juveniles and adults of *P. cygnus* are not found north or North West Cape (22°S) in Western Australia. However, collectors composed of artificial seaweed (Phillips 1972) positioned some 100 km north of the area caught numbers of pueruli of *P. cygnus* (B. F. Phillips, CSIRO, Australia).

## Larval Transport Between *Jasus* Populations Around the Southern Ocean

Some transport of larvae between individual populations of *Jasus* around the Southern Ocean appears feasible, but is unconfirmed. The island of Tristan da Cunha may supply larvae of *J. tristani* to Vema Seamont. Larval transport of Australian species of *Jasus* to New Zealand appears likely.

### Relationships and Distribution of *Jasus* Species

Six members of the genus *Jasus* show a fragmented, circumpolar distribution. The three species located on small oceanic islands in different oceans are more similar to each other morphologically than they are to the three closely related species distributed around continents and large islands. Seven species of *Jasus* occur in the temperate waters of the Southern Hemisphere (Fig. 3). The genus comprises two groups, the larger being the "*lalandii*" group of six morphologically very similar species. All of these were assigned formerly to *J. lalandii* until recognised as separate species by Holthuis (1963). Subsequent taxonomic studies (Holthuis and Sivertsen 1967; George and Kensler 1970) have now established two subgroups of the more closely related species within this group: a "*lalandii*" subgroup consisting of *J. lalandii* (South Africa), *J. novaehollandiae* (Australia), and *J. edwardsii* (New Zealand) and a "*frontalis*" subgroup consisting of *J. frontalis* (Juan Fernandez Islands), *J. paulensis* (Heller) (St. Paul and Amsterdam Islands), and *J. tristani* (Tristan da Cunha, Gough Island, and Vema Seamount). The other group consists of a single, and distinctly different, species, *J. verreauxi*, which is found on the east coast of Australia from New South Wales to South Australia, and occasionally in Tasmania (Hickman 1946), and around New Zealand, particularly the northeastern coast of the North Island (Kensler 1967).

The phyllosomata of *J. novaehollandiae* and *J. edwardsii* also are almost impossible to distinguish (McWilliam and

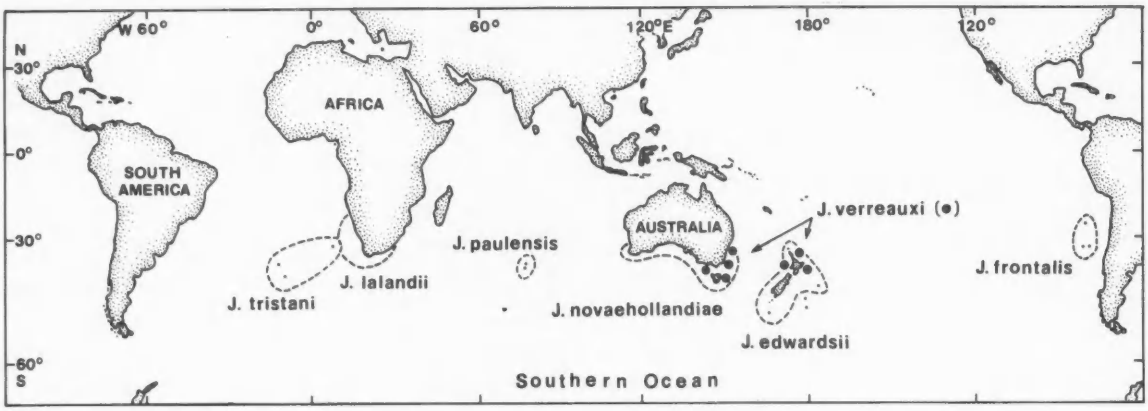


FIG. 3. Circumpolar distribution of spiny lobsters of the genus *Jasus*.

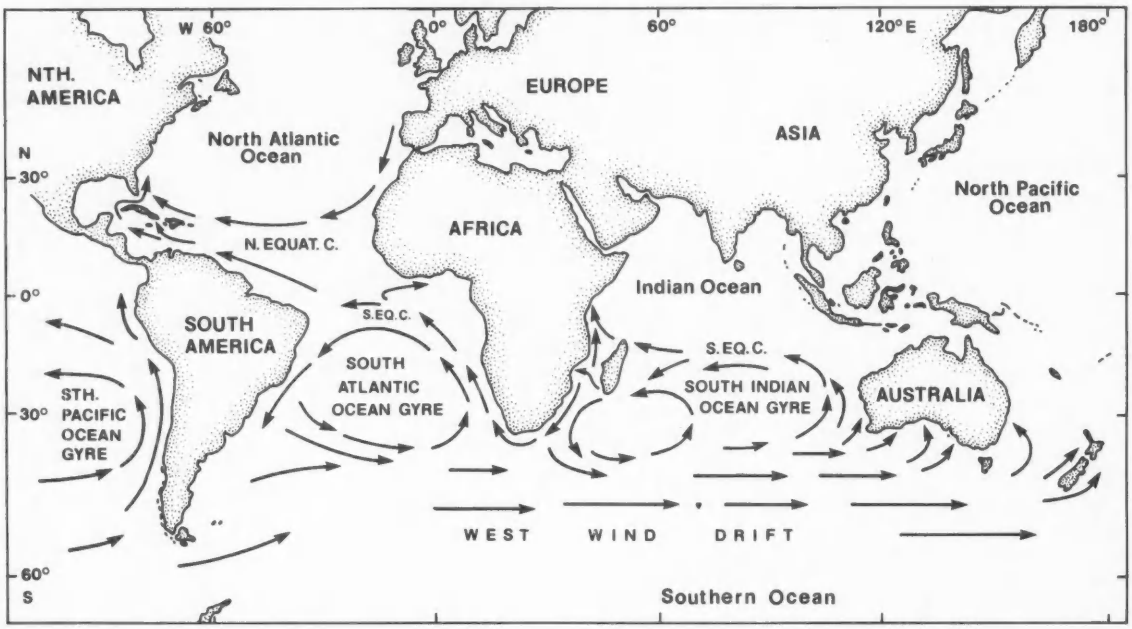


FIG. 4. Main oceanic circulation pattern in the southern latitudes as deduced from drift card returns (after Shannon et al. 1973).

Phillips 1986). Their larvae appear to resemble closely those of *J. lalandii* illustrated by Lazarus (1967), but inadequately described for comparative studies. However, the few late phyllosoma stages of *J. frontalis* that have been described (Baez 1973) and the final phyllosoma of *J. tristani* (Miller 1985) appear to differ slightly from their counterparts in the "*lalandii*" subgroup. The phyllosomata of *J. paulensis* have not been described.

## Transport Mechanisms in the Southern Ocean

The west wind drift is the main larval transport system around the Southern Ocean. The circumpolar distribution of the "*lalandii*" group of *Jasus* species, which is confined to southern temperate latitudes (approximately 34–45°S), can lead to their larvae being in the area affected by the uninterrupted flow of the Circumpolar Current or West Wind Drift, which influences the circulation of the whole Southern Ocean (Wyrtki 1960). The major oceanic circulation patterns in the higher Southern Hemisphere latitudes (Fig. 4), and the mean rates of flow of the major current systems in the Pacific, Atlantic, and Southern oceans have been estimated by Shannon et al. (1973) from drift card returns. The strength of the West Wind Drift varies with latitude from about 15 $cm \cdot s^{-1}$ at 40°S to about 27 $cm \cdot s^{-1}$ at 55°S.

Using the published drift rates of Shannon et al. (1973) and others, Edgar (1986) estimated that a floating object would be expected to travel from the longitudes of South America to the longitudes of South Africa in about 570 d, from South Africa to Australia in about 570 d, and from New Zealand to South America in about 770 d. This means that in the vicinity of 50°S latitude it would take about 4.3 yr for a floating surface object

to circumnavigate the Southern Ocean. Naturally, the latitude is critical. Harden Jones (1984), using a slightly higher latitude, estimated that a drifting larva of the southern bluefin tuna *Thunnus maccoyii* (Castlenau) might complete the circumnavigation in about 1.5 yr.

### Feasibility of Larval Transport

Some transport of larvae between populations of *Jasus* around the Southern Ocean appears feasible, but is unconfirmed. Obviously, phyllosomata are not passive drifting objects. Earlier in this review we described clearly the role of vertical movements of these larvae in the transport process. However, it would seem that the wind-driven surface currents of the Southern Ocean are the fastest transport mechanisms likely to transport phyllosomata in this area, while surface and subsurface currents contribute to transport in the same direction, but at a slower speed. Vertical movements taking the larvae away from the surface are likely, in this case, to reduce rather than speed up transport.

Using the data of Pollock (1973), *J. lalandii* may have a larval life of up to 19 mo (570 d), and Lesser (1978) and Booth (1979) estimated a maximum larval life of 22–23 mo (660–690 d) for *J. edwardsii*. Transport of individual larvae around the entire Southern Ocean is therefore unlikely. However, if the larval life of other species of *Jasus* is about as long as those estimated for *J. edwardsii* and *J. lalandii*, some larval transport between populations of *Jasus* around the Southern Ocean in the West Wind Drift appears feasible.

Local recruitment would appear to be necessary to sustain the population of *J. frontalis* on the Juan Fernandez Islands, *J. paulensis* on St. Paul and Amsterdam islands, and *J. tristani* on Tristan da Cunha. However, resolution of this question is impossible until more is known of the longevity and behaviour of their larvae in relation to undescribed fine-scale surface and subsurface flow in each region. In support of the local recruitment hypothesis for the three oceanic island populations, it is significant that they comprise a morphologically distinct subgroup from that of the other *Jasus* species. Bakun (1985) provided a detailed and interesting discussion of a number of hydrodynamic features of the oceans including "Taylor Columns" (Taylor 1917) which may be involved in maintaining local retention of larvae around oceanic islands. However, their role remains conjectural at this time.

### Recruitment to Vema Seamount

Larval recruitment to Vema Seamount is apparently effected from the populations on Tristan da Cunha and Gough Island. *Jasus tristani* occurs on the South Atlantic islands of Tristan da Cunha and Gough Island and on Vema Seamount (Heydorn 1969). The isolation of these islands and the situation of Vema Seamount approximately 2200 km to the east–northeast of Tristan da Cunha make the question of recruitment to the population of considerable interest. Heydorn (1969) suggested that larval transport from Tristan da Cunha and Gough Island to Vema Seamount occurred by larvae drifting in the South Atlantic Ocean gyre. An analysis of the drift of free-floating, satellite-tracked weather buoys (Lutjeharms and Heydorn 1981a) supports this hypothesis. Three South African weather buoys deployed in the southeastern Atlantic Ocean near Tristan da Cunha for the Global Weather Experiment reached the area of Vema Seamount in 146–227 d (Lutjeharms and Valentine 1981), well within the estimated longevity of the larvae, even allowing for slower subsurface transport of older stages.

### Larval Transport Between Australia and New Zealand

There is evidence to support the hypothesis of larval transport between Australia and New Zealand. The presence of *J. verreauxi* populations in both Australia and New Zealand and the morphological similarity of *J. novaehollandiae* and *J. edwardsii* have caused several authors to question the discreteness of the populations in the two countries and to ask whether the breeding stock of the Australian population of *J. verreauxi* could be a source for the New Zealand population of *J. verreauxi* (Williamson 1967; Winstanley 1970; Booth 1986).

Some electrophoretic studies, as well as field observations, support the above hypothesis. A genetic study of *J. edwardsii* from New Zealand and *J. novaehollandiae* from Tasmania, Australia, was carried out by Smith et al. (1980) using electrophoretic techniques. The genetic variation was so slight as to suggest that they are conspecific populations of a single species which have diverged only recently. The capture of *Jasus* phyllosomata midway across the Tasman Sea, the results of the electrophoretic examinations, and the quite high frequency of occurrence in New Zealand of adults with antennal banding (a characteristic of *J. novahollandiae* that is used to distinguish it from *J. edwardsii*) all point to the possibility that spiny lobsters in Australia can contribute larvae to New Zealand (J. D. Booth and R. J. Street, Ministry of Agriculture and Fisheries, New Zealand, pers. comm.).

## Role of the Puerulus in the Recruitment to the Benthic Stock

The puerulus stage completes the pelagic cycle. It fulfills a vital role in increasing the chances of progeny reaching their coastal settlement area, thus reinforcing recruitment to the benthic populations.

### Stimulus for Metamorphosis

There is a complete lack of information on the possible stimuli for metamorphosis of the final phyllosoma stage. Probable environmental stimuli can only be inferred from field observations of larval distributions. Mixing of coastal and oceanic waters occurs adjacent to all coastlines, and as shown previously, late phyllosoma stages are rarely, if ever, found near the coast (i.e. over the continental shelf). At the end of the larval period of its life cycle a stimulus, or series of stimuli, triggers metamorphosis of the final phyllosoma stage to the puerulus. Obvious stimuli for this metamorphosis are changes in temperature and/or salinity, either by mixing of the water containing the larvae with another water body or by movement of the larvae into another water body. For example, Booth (1980) suggested that, for *J. edwardsii*, metamorphosis to the puerulus was initiated by contact with less saline shelf water. Salinity rather than temperature is the more probable cause, as the daily vertical migrations of phyllosomata would normally subject them to a range of temperatures, whereas if they remain in the same water mass, the salinity would remain essentially constant.

Some recent field data indicate that the salinity range is likely to be more restrictive to phyllosomata distribution than

is the temperature range. Studies of the distribution of the larvae of scyllarid species in the Gulf of Carpentaria, northern Australia (P.C. Rothlisberg, CSIRO, Australia, pers. comm.) have shown that all stages of the phyllosomata of *Scyllarus martensii* Pfeffer were present in temperatures from 22 to 30°C, but in a salinity range of only $33 \times 10^{-3}$ to $34 \times 10^{-3}$, which suggests the importance of salinity, rather than temperature, to the larvae. Moreover, off southeastern Australia, some 15% of mid- to late-stage larvae of *P. longipes femristriga* were found outside the warm-core eddy in which they were transported from northern subtropical or tropical regions (McWilliam and Phillips 1983). Although the temperature of the eddy and the surrounding waters differed by >6°C, the salinity changes were less marked: in the order of $0.2 \times 10^{-3}$.

### Swimming Ability

The puerulus stage is well adapted for directional swimming and apparently capable of sustained swimming over considerable distances. The puerulus can swim forwards and backwards using its abdominal appendages, and its rapid (abdomen flex) advoidance movements are similar to those of the juvenile and adult stages (Berry 1974; Serfling and Ford 1975; Phillips and Olsen 1975). Swimming by the puerulus is directional and steady (Lyons 1980). Forward swimming speeds of 6–9 $cm \cdot s^{-1}$ were recorded for *P. interruptus* (Serfling and Ford 1975), 15–46 $cm \cdot s^{-1}$ (mean) for *P. cygnus* (Phillips and Olsen 1975), and 7.8 and 9.3 $cm \cdot s^{-1}$ for *P. argus* (Calinski and Lyons 1983).

The energetics of swimming behaviour of pueruli have not as yet been studied. However, they have been studied in similar Crustacea, including euphausiids. *Euphasia superba* Dana, which is approximately the same size and shape as a puerulus, also uses pleopod beating for normal forward swimming. It can maintain swimming speeds of between 3 and 13 $cm \cdot s^{-1}$ for several hours without increasing its standard hovering metabolism, and it is actually energetically more favourable for this euphausiid to swim at speeds of between 3 and 10 $cm \cdot s^{-1}$ than to hover on the spot. At 13 $cm \cdot s^{-1}$, it could travel 11 $km \cdot d^{-1}$ or 350 $km \cdot mo^{-1}$ (Kils 1981).

Studies of the pueruli of *P. cygnus* have shown that they swim 40–60 km across the shelf of Western Australia before settling in the shallow coastal reefs (Phillips et al. 1978; Phillips 1981). If the energetics of the pueruli of this and other palinurid species are similar to those of *E. superba*, clearly they would be capable of swimming greater distances, depending on the duration of the puerulus stage and prevailing currents in the area of settlement. The duration of the puerulus stage is unknown, but Sheard (1949) estimated a 2- to 3-wk period for *P. cygnus*, while Serfling and Ford (1975) suggested 2.5 mo for *P. interruptus*.

### Navigational Ability

It has been hypothesised that the puerulus is able to navigate towards the coast. The method by which the shoreward direction is determined is unknown, but as pointed out by Booth (1980), because of the small numbers of pueruli taken beyond the shelf edge, it seems unlikely that the puerulus stage undergoes a simple random dispersal after metamorphosis. Phillips and Penrose (1985) hypothesised that the puerulus uses underwater sound produced by waves or swell breaking on the shore, or the horizontal oscillation produced by the passage of waves or swell called "wave surge," as the clue to locate the shore. Phillips and MacMillan (1986) have identified a series of pinnate, interlocking hairs located on the antennae of the puerulus of *P. cygnus* and suggested that they may be the mechanism used to detect these stimuli.

Shanks (1985) demonstrated that often the megalopa stage of the crab *Pachygrapsus crassipes* Randall migrates from the offshore plankton back to the coast of California in slicks over tidally forced internal waves. Utilisation of this mode of transport requires that the organism remain at the ocean surface. This is not the case in the puerulus of *P. cygnus*, except within a few hundred metres of the shore. However, Steedman (1984) reported that long-period (20–120 s) surface gravity waves are a regular feature on the continental shelf of Western Australia throughout the year. If the puerulus stage of *P. cygnus* is capable of detecting these waves, they would provide a suitable clue to guide it to the coast.

## Discussion and Conclusions

Overall, it is the scale of larval transport and the role of the puerulus stage in the recruitment process of palinurid lobsters which have not been well understood. Sampling seldom can be carried out over the enormous distances the larvae are transported, and a synoptic picture of the circulation of such an area is not usually available. Most larvae are transported over hundreds of kilometres by wind-driven surface currents or deeper circulation currents or both. Some larvae may remain in coastal areas, and may provide some recruitment, but the majority are usually transported to areas further than 100 km offshore and they appear to be the principal source of recruits to the adult populations. After metamorphosis from the last phyllosoma stage, the puerulus swims long distances to the coast, thereby fulfilling a key role in the recruitment process.

It is clear from the study of *P. cygnus* that knowledge of the ontogenetic vertical movements of phyllosoma stages is essential if we are to have a full appreciation of transport mechanisms and recruitment processes in other palinurid species. The importance of obtaining data on vertical migrations of other species is emphasized, but this work should be combined with simultaneous long-term measurements of current speed and direction to discover the advection distances and direction of transport of the larvae. A study of wind-driven currents should be considered also.

Can we improve substantially our understanding of larval transport processes? Further progress will certainly be difficult and expensive. The section on *Jasus* in this review indicates the magnitude of the problem. Local recruitment to most populations is indicated, but unconfirmed, and we are a very long way from understanding how it occurs. The investigation of larvae that have an estimated larval life of possibly up to 23 mo and that are dispersed over wide areas is beyond the resources of most research programmes. The scale of larval distribution imposes tremendous difficulties in developing a synoptic picture of larval distribution in relation to circulation, and sampling from ships does not appear to be a practicable solution.

It is not possible to determine whether phyllosomata that eventually survive and settle are from a particular area or are those subject to a specific set of ocean circulation features. Existing tags and radioactive tracers are impracticable for the larvae and biochemical approaches have proved to be inconclusive partly because of the low genetic variability of crustaceans

(Hedgecock et al. 1977; Mulley and Latter 1980; Redfield et al. 1980; Menzies 1981; Shaklee and Samollow 1984; Salini et al. 1986). As Idyll (1981) pointed out, this vital issue must be resolved because management cannot be fully efficient until it is known if adjacent spiny lobster stocks are interconnected, separate, or somewhere between these extremes.

The development of drogues or satellite-tracked buoys that simulate the circadian vertical migration of phyllosomata should be investigated. This, combined with the rapid improvements in satellite oceanography, such as the microwave scatterometer sensors used aboard SEASAT-A to estimate wind stress at a resolution of 50 km, may provide some solutions. In addition, mathematical models of dispersal patterns are being developed (e.g. Rothlisberg et al. 1983) which may assist in the understanding of larval distribution. However, a detailed knowledge of the vertical movements and behaviour of the pelagic stages will be needed to make reliable predictions from such models. In addition, many of the models of circulation systems are two-dimensional and assume that the upper water layer (about 200 m) is an integrated body of water; therefore, they are probably inappropriate for determining larval transport.

None of the studies which we have examined in this review considered the possibility that juveniles or adults could walk over distances of the same magnitude as those invoked in larval transport. For instance, it was assumed that larval recruitment was responsible for the populations of *P. elephas* on the Norwegian coast. However, Bell et al. (1986) have found that *P. ornatus* regularly walk up to 500 km across Torres Strait into the Gulf of Papua, and Booth (1986) reports a tagged *J. verreauxi* walking 1070 km along the coast of New Zealand. The British Isles are surrounded by relatively shallow seas and would appear to provide no barrier to a similar movement of juveniles or adults of *P. elephas*. Nevertheless, larval recruitment is probably the most likely source of the Norwegian distribution of nonbreeding adults.

Our concept of larval recruitment of spiny lobsters has changed in recent years. The phyllosoma larval form is highly adapted for wide dispersal but its vertical migratory behaviour and longevity increase the chance of larval recruitment to the benthic stock. Mileykovskiy (1966) stated that larvae of most benthic invertebrates are practically incapable of moving horizontally at speeds greater than current velocities and are subject essentially to passive transport. This may be true for the gastropods and lamellibranchs he used as examples. However, the Palinuridae exhibit more complex larval behaviour and, in addition, have a nektonic puerulus stage in their pelagic cycle. Elimination of the necessity for the phyllosomata to be transported back to the point of settlement would appear to have given the palinurid lobsters a major advantage. The success of the spiny lobsters as a group usually has been attributed to their high fecundity and also their long larval life. We believe that equal emphasis should be placed on the role of the unique puerulus stage in the recruitment process. The perpetuation of palinurid populations, and especially those on isolated, oceanic islands, would seem to depend on the behaviour and mobility of the puerulus stage.

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## References

BAEZ, P. R. 1973. Larvas phyllosoma del pacifico sur oriental (Crustacea, Macrura, Scyllaridea). Rev. Biol. Mar. Valparaiso. 15(1): 115–130.

1983. Larvas phyllosoma y puerulus de la langosta verde *Panulirus gracilis* Streets 1871 procedentes de la expedicion Costa Rica, 1973 (Crustacea: Decapoda: Palinuridae). Rev. Biol. Mar. Valparaiso. 19(1): 79–111.

BAKUN, A. 1986. Local retention of planktonic early life stages in tropical reef/bank demersal systems: the role of vertically-structured hydrodynamic processes? *In* Report of the IREP (OSLR) Workshop on Recruitment in Tropical Coastal Demersal Communities, Ciudad del Carmen, Mexico.

BELL, R. S., P. W. CHANNELLS, W. MACFARLANE, R. MOORE, AND B. F. PHILLIPS. 1986. Movements and breeding of the ornate rock lobster *Panulirus ornatus* in Torres Strait and on the northeast coast of Queensland. Aust. J. Mar. Freshwater Res. (In press)

BERRY, B. F. 1974. A revision of the *Panulirus homarus* group of spiny lobsters (Decapoda, Palinuridae). Crustaceana 27: 31–42.

BOOTH, J. D. 1979. Settlement of the rock lobster, *Jasus edwardsii* (Decapoda: Palinuridae), at Castlepoint, New Zealand. N.Z. J. Mar. Freshwater Res. 13: 395–406.

1980. Larval recruitment studies. Catch '80, 7(7): 22–23.

1986. Recruitment of packhorse rock lobster *Jasus verreauxi* in New Zealand. Can. J. Fish. Aquat. Sci. 43: 2212–2220.

BOOTH, J. D., AND S. C. TARRING. 1982. Settlement of larval rock lobsters. Catch '82, July: 10–14.

BRAINE, S. J., D. W. RIMMER, AND B. F. PHILLIPS. 1979. An illustrated key and notes on the phyllosoma stage of the western rock lobster *Panulirus cygnus* George. CSIRO Div. Fish. Oceanogr. Rep. 102: 1–13.

CALINSKI, M. D., AND W. G. LYONS. 1983. Swimming behavior of the puerulus of the spiny lobster *Panulirus argus* (Latreille, 1804) (Crustacea, Palinuridae). J. Crustacean Biol. 3(3): 329–335.

CHITTLEBOROUGH, R. G. 1970. Studies on recruitment in the Western Australian rock lobster *Panulirus longipes cygnus* George: density and natural mortality of juveniles. Aust. J. Mar. Freshwater Res. 21: 131–148.

CHITTLEBOROUGH, R. G., AND L. R. THOMAS. 1969. Larval ecology of the Western Australian marine crayfish with notes upon other panulurid larvae from the eastern Indian Ocean. Aust. J. Mar. Freshwater Res. 26: 317–328.

CRESSWELL, G. R. 1972. Wind driven ocean surface transport around Australia. Rep. Div. Oceanogr. CSIRO. Aust. No. 52: 1–8.

CRESSWELL, G. R., AND T. J. GOLDING. 1980. Observations of a south-flowing current in the south eastern Indian ocean. Deep-Sea Res. 27A: 449–466.

CUTLER, A. N., AND J. C. SWALLOW. 1984. Surface currents of the Indian Ocean (to 25°S, 100°E) I.O.S. 187 Institute of Oceanographic Sciences, Wormley. 7 p + charts.

DEFANT, A. 1961. Physical oceanography. Vol. 1. Pergamon, Oxford. 729 p.

EDGAR, G. J. 1986. Biogeographical processes in the Southern Hemisphere marine environment. Medio Ambiente. (In press)

GEORGE, R. W., AND L. B. HOLTHUIS. 1965. A revision of the Indo-West Pacific spiny lobsters of the *Panulirus japonicus* group. Zool. Verh. (Leiden) 71: 1–36.

GEORGE, R. W., AND C. B. KENSLER. 1970. Recognition of marine spiny lobsters of the *Jasus lalandii* group (Crustacea: Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 4(3): 292–311.

GODFREY, J. S., AND K. R. RIDGWAY. 1985. The large-scale environment of the poleward-flowing Leeuwin Current, Western Australia: longshore steric height gradients, wind stresses and geostrophic flow. J. Phys. Oceanogr. 15: 481–495.

GRUNDLINGH, M. L. 1983. Eddies in the southern Indian Ocean and Agulhas Current, p. 245–264. *In* A. Robinson [ed.] Eddies in marine science. Springer-Verlag, Berlin.

GUERRA, M., AND M. GAUDENGIO. 1982. First capture of S.W. African crayfish *Jasus lalandii* on the Portuguese coast. Mem. Mus. Mar. (Inst. Nac. Invest. Pescas) Ser. Zool. 2(22): 1–12.

HAMON, B. V. 1965. Geostrophic currents in the south-eastern Indian Ocean. Aust. J. Mar. Freshwater Res. 16: 255–271.

HARDEN JONES, F. R. 1984. A view from the ocean, p. 1–26. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neill [ed.] Mechanisms of migration in fishes. Plenum Publishing Corp., New York, NY.

HASUNUMA, K., AND K. YOSHIDA. 1978. Splitting of the subtropical gyre in the

western North Pacific. J. Oceanogr. Soc. Jpn. 34: 160–172.

HEDGECOCK, D., K. NELSON, J. SIMMONS, AND R. SHLESER. 1977. Genetic similarity of American and European species of the lobster *Homarus*. Biol. Bull. 152: 41–50.

HEWITT, R. 1981. Eddies and speciation in the California current. Cal CO FI Rep. 22: 96–98.

HEYDORN, A. E. F. 1969. The South Atlantic rock lobster *Jasus tristani* at Vema Seamount, Gough Island and Tristan da Cunha. Invest. Rep. Div. Sea Fish. S. Afr. 73: 1–20.

1978. Ecology of the Agulhas Current region: an assessment of biological responses to environmental parameters in the south-west Indian Ocean. Trans. R. Soc. S. Afr. 43(2): 151–190.

HICKMAN, V. V. 1946. Notes on the Tasmanian marine crayfish, *Jasus lalandii* (Milne-Edwards). Pap. Proc. R. Soc. Tas. 1954: 27–38.

HOLTHUIS, L. B. 1963. Preliminary descriptions of some new species of Palinuridae (Crustacea, Decapoda, Macrura, Reptantia). Proc. K. Ned. Akad. Wet. Ser. C Biol. Med. Sci. (Sect. C) 66: 54–60.

HOLTHUIS, L. B., AND E. SIVERTSEN. 1967. The Crustacea, Decapoda, Mysidacea and Cirripedia of the Tristan da Cunha Archipelago with a revision of the "*frontalis*" subgroup of the genus *Jasus*. Results Norw. Sci. Exped. Tristan da Cunha 1937–38, 52: 1–55.

IDYLL, C. P. 1981. Summary and importance of the GCFI sessions on spiny lobsters. Proc. Gulf Caribb. Fish. Inst. 33: 322–335.

INGLE, R. M., B. ELDRED, H. W. SIMS, AND E. A. ELDRED. 1963. On the possible Caribbean origin of Florida spiny lobster populations. Fla. Board Conserv. Mar. Res. Lab. Tech. Ser. 40: 1–13.

JACKSON, G. A., AND R. R. STRATHMANN. 1981. Larval mortality from offshore mixing as a link between precompetent and competent periods of development. Am. Nat. 118: 16–26.

JENKS, W. N., J. GRINDROD, AND J. A. PETERSON. 1982. Drift currents in the southern New Zealand region as derived from Lagrangian measurements and the remote sensing of sea-surface temperature distributions. N.Z. J. Mar. Freshwater Res. 16: 359–371.

JOHNSON, M. W. 1960a. The offshore drift of larvae of the California spiny lobster, *Panulirus interruptus*. Calif. Coop. Oceanic Fish. Invest. Rep. 7: 147–161.

1960b. Production and distribution of larvae of the spiny lobster, *Panulirus interruptus* (Randall) with records of *P. gracilis* Streets. Bull. Scripps Inst. Oceanogr. Univ. Calif. 7: 413–446.

1971. The palinurid and scyllarid lobster larvae of the tropical eastern Pacific and their distribution as related to the prevailing hydrography. Bull. Scripps Inst. Oceanogr. Univ. Calif. 19: 1–36.

1974. On the dispersal of lobster larvae into the east Pacific barrier (Decapoda, Palinuridae). Fish. Bull. 72: 639–647.

JOHNSON, M. W., AND E. BRINTON. 1963. Biological species, water-masses and currents, p. 381–403. *In* M. L. Hill [ed.] The sea. Ideas and observations on progress in the study of the seas. Vol. 2. The composition of seawater and comparative and descriptive oceanography. Interscience Publishers, London.

KANCIRUK, P. 1980. Ecology of juvenile and adult Palinuridae (spiny lobsters), p. 59–96. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol II. Academic Press, New York, NY.

KENSLER, C. B. 1967. The distribution of spiny lobsters in New Zealand waters (Crustacea: Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 1: 412–420.

KILS, U. 1981. The swimming behavior, swimming performance and energy balance of Antarctic krill, *Euphausia superba*. Biomass Sci. Ser. 3: 1–121.

LAI, D., AND P. L. RICHARDSON. 1977. Distribution and movement of Gulf Stream rings. J. Phys. Oceanogr. 7(5): 670–683.

LAZARUS, B. I. 1967. The occurrence of phyllosomata off the Cape with particular reference to *Jasus lalandii*. S. Afr. Div. Sea Fish. Invest. Rep. 63.

LESSER, J. H. R. 1974. Identification of early larvae of New Zealand spiny and shovel-nosed lobsters (Decapoda, Palinuridae and Scyllaridae). Crustaceana 27: 259–277.

1978. Phyllosoma larvae of *Jasus edwardsii* (Hutton) (Crustacea: Decapoda: Palinuridae) and their distribution off the east coast of the North Island, New Zealand. N.Z. J. Mar. Freshwater Res. 12: 357–370.

LEWIS, R. K. 1977. Rock lobster puerulus settlement in the south-east. SAFIC 13: 9–11.

LITTLE, J. JR. 1977. Observations on recruitment of post-larval spiny lobsters, *Panulirus argus* to the south Florida coast. Fla. Mar. Res., Publ. 29: 1–35.

LUTJEHARMS, J. R. E., AND A. E. F. HEYDORN. 1981a. The rock lobster *Jasus tristani* on Vema Seamount: drifting buoys suggest a possible recruiting mechanism. Deep-Sea Res. 28: 631–636.

1981b. Recruitment of rock lobster on Vema Seamount from the islands of Tristan da Cunha. Seep-Sea Res. 28A (10): 1237.

LUTJEHARMS, J. R. E., AND H. R. VALENTINE. 1981. Ocean circulation studies in the vicinity of southern Africa: preliminary results using FGGE drifters and remote sensing. Adv. Space Res. 1: 211–223.

LYONS, W. G. 1970. Scyllarid lobsters (Crustacea, Decapoda). Mem. Hourglass Cruises 1: 1–74.

1980. The postlarval stage of scyllaridean lobsters. Fisheries 5(4): 47–49.

MACDONALD, C. D. 1986. Recruitment of the puerulus of the spiny lobster, *Panulirus marginatus*, in Hawaii. Can. J. Fish. Aquat. Sci. 43: 2118–2125.

MARCHAL, E. G. 1968. Sur la capture de long des cotes Africaines de deux specimens de *Panulirus argus* (Latrelle). Bull. Mus. Nat. Hist. Nat. 39: 1120–1122.

MCLELLAN, H. J. 1965. Elements of physical geography. Pergamon Press, London. 151 p.

MCWILLIAM, P. S., AND B. F. PHILLIPS. 1983. A study of phyllosoma larvae and other crustacean macroplankton associated with Eddy 'J' a warm-core eddy off south-eastern Australia. Aust. J. Mar. Freshwater Res. 34: 653–663.

1986. Distinguishing the phyllosoma larvae of rock lobster species of the genus *Jasus* (Decapoda: Palinuridae) in the waters of Australia and New Zealand. Crustaceana. (In press)

MENZIES, R. A. 1981. Biochemical population genetics and the spiny lobster larval recruitment problem: an update. Proc. Gulf Caribb. Fish. Inst. 33: 207–229.

MILEYKOVSKIY, S. A. 1966. Range of dispersion of the pelagic larvae of benthic invertebrates by currents and the migratory role of this dispersion taking Gastropoda and Lamellibranchia as examples. Okeanologia 3: 482–492.

MILLER, D. G. M. 1985. A late phyllosoma larva of *Jasus tristani* Holthuis (Decapoda, Palinuridea). Crustaceana 50(1): 1–6.

MOORE, R., AND J. W. MACFARLANE. 1984. Migration of the ornate rock lobster, *Panulirus ornatus* (Fabricius) in Papua New Guinea. Aust. J. Mar. Freshwater Res. 35: 197–212.

MULLEY, J. C., AND B. D. H. LATTER. 1980. Genetic variation and evolutionary relationships within a group of thirteen species of penaeid prawns. Evolution 34: 904–916.

NILSSON, C. S., AND G. R. CRESSWELL. 1981. The formation and evolution of East Australian current eddies. Prog. Oceanogr. 9: 133–183.

OWEN, R. W. 1980. Eddies of the California Current system: physical and ecological characteristics, p. 237–263. *In* D. M. Power [ed.] The California Islands. Proc. Multidisciplinary Symp., Santa Barbara Mus. Nat. Hist., Santa Barbara, CA.

1981. Fronts and eddies in the sea: mechanisms, interactions and biological effects, p. 197–233. *In* A. R. Longhurst [ed.] Analysis of marine ecosystems. Academic Press, London.

PARKER, K. P. 1972. Recruitment and behaviour of puerulus larvae and juveniles of the California spiny lobster, *Panulirus interruptus*. Master's thesis, Dan Diego State University, San Diego, CA. 91 p.

PEARCE, A., AND G. CRESSWELL. 1985. Ocean circulation of Western Australia and the Leeuwin Current. CSIRO Div. Oceanogr. Inf. Sheet 16–3: 4 p.

PHILLIPS, B. F. 1972. A semi-quantitative collector of the puerulus larvae of the western rock lobster *Panulirus longipes cygnus* George (Decapoda, Palinuridae). Crustaceana 22: 147–154.

1975a. The effect of nocturnal illumination on catches of the puerulus stage of the western rock lobster by artificial seaweed collectors. Aust. J. Mar. Freshwater Res. 26: 411–414.

1975b. The effect of water currents and the intensity of moonlight on catches of the puerulus stage of the western rock lobster. CSIRO Div. Fish. Oceanogr. Rep. 63: 1–9.

1981. The circulation of the south eastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

PHILLIPS, B. F., R. S. BELL, P. W. CHANNELLS, W. D. DALL, AND G. P. KIRKWOOD. 1983. Tropical rock lobster *Panulirus ornatus*. Report on CSIRO research from 1980–1983. CSIRO Marine Laboratories, Marmion, Western Australia. p. 129.

PHILLIPS, B. F., P. A. BROWN, D. W. RIMMER, AND S. J. BRAINE. 1981. Description, distribution and abundance of the late larval stages of the Scyllaridae (slipper lobsters) in the south-eastern Indian Ocean. Aust. J. Mar. Freshwater Res 32: 417–437.

PHILLIPS, B. F., P. A. BROWN, D. W. RIMMER, AND D. D. REID. 1979. Distribution and dispersal of the phyllosoma larvae of the western rock lobster *Panulirus cygnus* in the south eastern Indian ocean. Aust. J. Mar. Freshwater Res. 20: 773–783.

PHILLIPS, B. F., J. S. COBB, AND R. W. GEORGE. 1980. Chapter 1. General biology, p. 1–82. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. I. Physiology and behaviour. Academic Press, New York, NY.

PHILLIPS, B. F., AND N. G. HALL. 1978. Catches of puerulus larvae on collectors as a measure of natural settlement of the western rock lobster *Panulirus cygnus* George. CSIRO Aust. Div. Fish. Oceanogr. Rep. 98: 1–18.

PHILLIPS, B. F., AND D. L. MACMILLAN. 1986. The antennal receptors in puerulus and post-puerulus stages of the rock lobster *Panulirus cygnus* (Decapoda, Palinuridae) and their potential role in puerulus navigation. J. Crustacean Biol. (In press)

PHILLIPS, B. F., AND P. S. MCWILLIAM. 1986. Phyllosoma larvae and the ocean currents off the Hawaiian Islands. Pac. Sci. (In press)

PHILLIPS, B. F., AND L. OLSEN. 1975. Swimming behavior of the puerulus larvae of the western rock lobster. Aust. J. Mar. Freshwater Res. 26: 415–417.

PHILLIPS, B. F., AND J. D. PENROSE. 1985. The puerulus stage of the spiny (rock) lobster and its ability to locate the coast. School of Physics and Geosciences, Western Australian Institute of Technology Report No. SPG 374/1985/AP92.

PHILLIPS, B. F., D. W. RIMMER, AND D. D. REID. 1978. Ecological investigations of the late stage phyllosoma and puerulus larvae of the western rock lobster *Panulirus longipes cygnus*. Mar. Biol. 45: 347–357.

PHILLIPS, B. F., AND A. N. SASTRY. 1980. Chapter 2. Larval ecology, p. 11–57. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. II. Ecology and management. Academic Press, New York, NY.

POLLOCK, D. E. 1973. Growth of juvenile rock lobster *Jasus lalandii*. Sea Fish. Invest. Rep. 106: 16 p.

POLLOCK, D. E., AND P. C. GOOSEN. 1983. Phyllosoma larvae survey for west coast rock lobsters. S. Afr. J. Sci. 79: 144.

RAE, B. B., AND J. M. LAMONT. 1963. Rare marine invertebrates found in the Scottish area. Scott. Nat. 71(1): 23–28.

RAYMONT, J. E. G. 1983. Plankton and productivity in the oceans. Vol. 2. Zooplankton, 2nd ed. Pergamon Press, Oxford. 824 p.

REDFIELD, J. A., D. HEDGECOCK, K. NELSON, AND J. P. SALINI. 1980. Low heterozygosity in tropical crustaceans of Australia and the trophic stability hypothesis. Mar. Biol. Lett. 1: 303–313.

RICHARDS, W. J., AND J. R. GOULET. 1977. An operational surface drift model used for studying larval lobster recruitment and dispersal. *In* H. B. Steward, Jr. [ed.] Cooperative investigations of the Caribbean and adjacent regions. II. F.A.O. Fish. Rep. 200: 363–374.

RIMMER, D. W. 1980. Spatial and temporal distribution of early-stage phyllosoma of western rock lobster, *Panulirus cygnus*. Aust. J. Mar. Freshwater Res. 31: 485–497.

RIMMER, D. W., AND B. F. PHILLIPS. 1979. Diurnal migration and vertical distribution of phyllosoma larvae of the western rock lobster, *Panulirus cygnus* George. Mar. Biol. 54: 109–124.

ROBINSON, M. K. 1969. Theoretical predictions of subtropical countercurrent confirmed by bathythermograph (BT) data. Bull. Jpn. Soc. Fish Oceanogr. Spec. No. (Professor Uda's Commemorative Papers): 115–121.

ROTHLISBERG, P. C., J. A. CHURCH, AND A. M. G. FORBES. 1983. Modelling the advection of vertically migrating shrimp larvae. J. Mar. Res. 41: 511–538.

SALINI, J., G. RINTOUL, J. B. SHAKLEE, AND B. F. PHILLIPS. 1986. An electrophoretic analysis of stock structure in the ornate tropical rock lobster, *Panulirus ornatus*. *In* Proceedings of the Torres Strait Fisheries Seminar, 11–14 Feb., 1985.

SASTRY, A. N. 1983. Pelagic larval ecology and development, p. 213–282. *In* F. J. Vernberg and N. B. Vernberg [ed.] The biology of Crustacea. Vol. 7. Behaviour and ecology. Academic Press, New York, NY.

SERFLING, S. A., AND R. F. FORD. 1975. Ecological studies of the puerulus larval stage of the California spiny lobster, *Panulirus interruptus*. Fish. Bull. 73: 360–367.

SHAKLEE, J. B., AND P. B. SAMOLLOW. 1984. Genetic variation and population structure in a spiny lobster, *Panulirus marginatus*, in the Hawaiian Archipelago. Fish. Bull. 82(4): 693–702.

SHANKS, A. L. 1985. Behavioural basis forms internal-wave-induced shoreward transport of megalopae of the crab *Pachygrapsus crassipes*. Mar. Ecol. Prog. Ser. 24(3): 289–295.

SHANNON, L. V., G. H. STANDER, AND J. A. CAMPBELL. 1973. Oceanic circulation deduced from plastic drift cards. Sea Fish. Branch Invest. Rep. 108: 1–31.

SHEARD, K. 1949. The marine crayfishes (spiny lobsters), family Palinuridae, of Western Australia with particular reference to the fishery on the Western Australian crayfish (*Panulirus longipes*). CSIRO Aust. Div. Fish. Oceanogr. Bull. 247: 45 p.

SMITH, P. J., J. L. MCKOY, AND P. J. MACHIN. 1980. Genetic variation in the rock lobsters *Jasus edwardsii* and *Jasus novaehollandiae*. N.Z. J. Mar. Freshwater Res. 14(1): 55–63.

STEEDMAN, R. K. 1984. Some aspects of local to mesoscale oceanography Abrolhos Island area. *In* B. Hatcher and D. Walker [ed.] Proceedings of a Workshop on the Houtman Abrolhos. W. A. Branch of the Aust. Mar. Sci. Assoc. (Abstract)

SVERDRUP, H. U., M. W. JOHNSON, AND R. H. FLEMING. 1942. The oceans, their physics, chemistry and general biology. Prentice Hall, New York, NY. 1087 p.

TAMBS-LYCHE, H. 1958. Zoogeographical and faunistic studies on west Norwegian marine animals. Univ. Bergen Arbok Naturvitensk. Rekke 7(22): 1–24.

TAYLOR, G. I. 1971. Motion of solids in fluids when the flow is not irrotational. Proc. R. Soc. Lond. Ser. A Math. Phys. Sci. 93: 99–113.

THORSON, G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents, p. 455–474. *In* M. Sears [ed.] Oceanography; invited lectures presented at the International Oceanographic Congress held in New York, 31 Aug. – 12 Sept. 1959. Am. Assoc. Adv. Sci. Publ. 67, Washington, DC.

WEBSTER'S THIRD NEW INTERNATIONAL DICTIONARY OF THE ENGLISH LANGUAGE. 1981. Unabridged. Merriam-Webster Inc., Chicago, IL. 2662 p.

WILLIAMSON, D. I. 1967. Some recent advances and outstanding problems in the study of larval Crustacea. Marine Biological Society of India Symposium on Crustacea. p. 815–823.

1982. Larval morphology and diversity, p. 43–110. *In* L. G. Abele [ed.] The biology of crustacea. Vol. 2. Academic Press, New York, NY.

WINSTANLEY, R. H. 1970. Rock lobster larvae in the Tasman Sea. Tasmanian Fish. Res. 4(2): 11–12.

WYRTKI, K. 1960. The surface circulation in the Coral and Tasman Seas. CSIRO Aust. Div. Fish. Oceanogr. Tech. Pap. 8.

1962. Geopotential topographies and associated circulation in the south-eastern Indian Ocean. Aust. J. Mar. Freshwater Res. 13: 1–17.

# La répartition horizontale et verticale des larves de homard (*Homarus americanus*) autour des îles de la Madeleine, golfe du Saint-Laurent

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Trente-neuf stations localisées autour de l'extrémité est des îles de la Madeleine, dans deux lagunes et dans la baie de Plaisance ont été échantillonnées au cours des étés 1978, 1980 et 1981 au moyen de traits de filet à plancton. Des traits de surface à l'aide de filets simples (1978 et 1980) ou à l'aide d'un filet à trois compartiments superposés (1981) ont permis d'évaluer la répartition horizontale et verticale de chacun des quatre stades larvaires de *Homarus americanus*. L'essentiel de la production des larves de stade I s'effectue dans les régions sud-est et nord-est. L'abondance des larves de stades plus avancés est cependant faible au sud-est et pratiquement nulle au nord-est. Par contre, la baie de Plaisance recèle peu de larves de stade I, mais une très forte proportion de larves de stades III et IV. Les périodes d'apparition et d'abondance maximale de chaque stade sont aussi décalées pour les trois régions, étant plus précoces au nord-est qu'au sud-est et que dans la baie de Plaisance. Ces résultats suggèrent que le schéma général d'abondance des larves correspond au régime de courant, contournant la pointe de l'Est et concentrant des larves dans la baie de Plaisance par un mouvement giratoire des eaux. À une échelle plus fine, 12 stations formant une grille de 3 sur 4 stations dans la baie de Plaisance ont été échantillonnées durant 12 sem en été 1980. Les trois premiers stades ont une répartition fortement agrégée et sont principalement retrouvés à l'entrée de la baie. Par contre, les larves de stade IV sont retrouvées plus fréquemment à proximité du littoral et au fond de la baie. Il existe une corrélation significative entre l'abondance des larves de stade IV et la proximité des fonds rocheux favorables à la vie benthique. La répartition verticale des larves à deux stations en 1981 montre que seules les larves de stade I ont une répartition verticale dépendante de l'intensité lumineuse, étant présentes en plus grande abondance dans la couche de surface (0–0,8 m) à l'aube et au crépuscule. Elles étaient uniformément réparties entre 0 et 1,6 m durant le jour et jusqu'à 2,4 m durant la nuit. Les larves de stades II, III et IV étaient retrouvées près de la surface dans toutes les conditions.

Thirty-nine stations localized around the eastern tip of the Îles de la Madeleine, in two lagoons, and in the baie de Plaisance were sampled using plankton net tows during the summers of 1978, 1980, and 1981. The horizontal and vertical distributions of each of the four larval stages of *Homarus americanus* were assessed from sets of surface tows using simple neuston and meter nets (1978 and 1980) as well as a three-compartment plankton net (1981). Most of the stage I larval production takes place in the northeast and southeast regions. However, the abundance of stage IV larvae is low in the southeast and almost nil in the northeast. By contrast, the baie de Plaisance harbors very few stage I larvae, but a very high proportion of stage III and IV larvae. The periods of first appearance and maximum abundance are also out of phase for the three regions, occurring in the northeast before the southeast and the baie de Plaisance. These results suggest that the general pattern of abundance of larvae is driven by the current regime, flushing the larvae around the Pointe de l'Est and concentrating them in the baie de Plaisance following a gyre. On a smaller scale, 12 stations arranged in a 3 × 4 grid in the baie de Plaisance were sampled for 12 wk in the summer of 1980. The first three larval stages show a strongly aggregated distribution and are most frequent at the mouth of the bay. Conversely, stage IV larvae are found more frequently in the shore stations and inside the bay. There is a significant correlation between stage IV larval abundance and the distance to rocky bottoms favorable to benthic life. The vertical distribution of larvae at two stations (1981) shows that only the stage I larvae have a vertical distribution related to light intensity, being found in highest

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abundance in the surface layer (0–0.8 m) at dusk and dawn. Stage I larvae were uniformly distributed between 0 and 1.6 m during the day and down to 2.4 m at night. Stage II, III, and IV larvae were always found near the surface.

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L'abondance et la répartition spatiale des larves de homard ont été étudiées dans le détroit de Northumberland (Templeman 1936, 1937; Scarratt 1964, 1973), dans la baie Saint-Georges (Harding *et al.* 1982), sur les côtes de Terre-Neuve (Templeman et Tibbo 1945; Ennis 1983), ainsi que sur la côte ouest de la Nouvelle-Écosse (Stasko et Gordon 1983). Les travaux entrepris sur la côte est du Canada ont été revus par Stasko (1980), tandis que Fogarty (1983) en a fait la synthèse pour la côte est des États-Unis. Bien que touchant des secteurs assez éloignés les uns des autres, tous ces travaux rapportent la très faible densité des larves dans le milieu et en particulier la sous-représentation des larves des stades avancés (III et IV).

Outre leur faible densité, la répartition horizontale très irrégulière des larves est un second facteur entravant l'efficacité de leur échantillonnage. Plusieurs auteurs suggèrent que le transport horizontal des larves est principalement attribuable aux conditions hydrographiques, qu'il s'agisse de courants de surfaces engendrés par le vent (Ennis 1983), de courants giratoires à grande échelle ou de cellules de circulation de Langmuir (Harding *et al.* 1982).

La migration verticale entre des masses d'eau superposées se dirigeant dans des directions différentes est un autre mécanisme pouvant expliquer les déplacement horizontaux des larves planctoniques (Caddy 1979).

Au cours du quatrième stade planctonique, la larve se met à exécuter des plongeons vers le fond, possiblement pour trouver un fond propice à la vie benthique (Scarratt 1973; Bertran *et al.* 1985). Les larves de stade IV peuvent retarder leur mue et prolonger leur existence planctonique en l'absence d'un fond favorable (Cobb 1968), démontrant une nette préférence pour les fonds de pierre ou de gravier grossier (Pottle et Elner 1982). Aux îles de la Madeleine, les fonds rocheux favorables au homard occupent environ 10 % de la superficie totale, le reste étant principalement composé de fonds de sable (Sanschagrin 1964; Dubé 1984).

La préférence des larves pour certains types de fonds ainsi que la relative rareté de ces fonds aux îles de la Madeleine suggèrent l'existence d'un mécanisme permettant aux larves d'orienter leur déplacement. Bien que les réactions des larves à la température (Templeman 1936), la salinité (Scarratt et Raine 1967), la pression (Ennis 1975), la qualité (Hadley 1908) et l'intensité lumineuse (Ennis 1975) aient été étudiées en laboratoire, on ignore la nature exacte des stimuli guidant les larves dans leurs déplacements.

L'augmentation de la quantité de débris en suspension, la diminution de la transparence ainsi que le réchauffement des eaux près des côtes sont trois facteurs physiques dont le gradient pourrait servir d'indication aux larves quant à la direction de leurs mouvements. Outre l'orientation en fonction d'un gradient spatial, ces variables pourraient avoir un effet positif sur les larves lorsqu'elles atteignent la proximité de la côte, en y favorisant l'accumulation de proies utilisant les débris de zostère, en diminuant la susceptibilité visuelle aux prédateurs et en augmentant leur taux de croissance.

Par ailleurs, les études portant sur l'abondance et la répartition des larves de homard ont principalement utilisé des échantillonnages concentrés dans la couche de surface (0–1,0 m) durant le jour, conditions dans lesquelles les larves ont été prélevées en plus grande abondance (voir la revue de Stasko 1980). Cependant, plusieurs auteurs ont noté que la concentration de larves en surface était observée en conditions de lumière diffuse, soit par temps couvert le jour ou encore au cours des nuits de pleine lune (Templeman 1939). Par contre, on observait une plus grande répartition en profondeur en conditions de lumière intense ou d'obscurité totale (Templeman 1939; Templeman et Tibbo 1945; Harding *et al.* 1982). Les mouvement verticaux des populations larvaires selon différentes conditions lumineuses auraient donc possiblement biaisé les estimations de production des différents stades larvaires.

Ce travail intègre les résultats de trois saisons d'échantillonnage de larves de homard aux îles de la Madeleine en 1978, 1980 et 1981. Les échantillonnages de 1978 et 1980 avaient pour but d'étudier la répartition spatio-temporelle des larves autour de la pointe de l'Est et dans la baie de Plaisance, respectivement, comparant les schémas obtenus avec les données disponibles sur le schéma de circulation des eaux autour des îles. Nous utilisons aussi les données de 1980 pour étudier les relations entre la densité des larves de stade IV et la température, la transparence, la densité de débris de zostère ainsi que la distance des fonds rocheux propices à la vie benthique. La saison de 1981 examine plus en détail la répartition verticale des larves des quatre stades à deux stations où de fortes densités de larves avaient été précédemment notées; elle sert aussi à étudier la relation entre les densités observées et l'heure du jour, ainsi que l'intensité lumineuse.

## Site d'étude

Les îles de la Madeleine sont situées au sud du chenal Laurentien dans le golfe du Saint-Laurent, au centre du plateau continental peu profond bordant la face nord de l'île du Prince Édouard (fig. 1). Le corps principal de l'archipel est composé de sept îles reliées par d'étroites dunes sablonneuses orientées selon l'axe NE–SW. La pointe de l'Est et la dune du Nord forment un segment rectiligne se terminant en un vaste crochet formé de la baie de Plaisance et de l'île d'Entrée au sud-ouest.

La circulation des eaux de surface dans cette région montre un déplacement du nord-ouest vers le sud-est, la face nord des îles recevant des masses d'eau en provenance du courant de Gaspé et de la baie de Miramichi (Bumpus et Lauzier 1965). Ces masses d'eau contournent les extrémités des îles et se dirigent vers la péninsule du Cap-Breton (El-Sabh 1976). De ce schéma général résulte probablement une circulation plus lente, de type giratoire, sur la face sud des îles. En effet, des dériveurs de surface lâchés dans le secteur de Grosse Île (nord-est des îles) ont contourné la pointe de l'Est pour ensuite se diriger vers le sud (Anonyme 1978b). Les sites de concentration et les configurations de mouvements des glaces correspondent

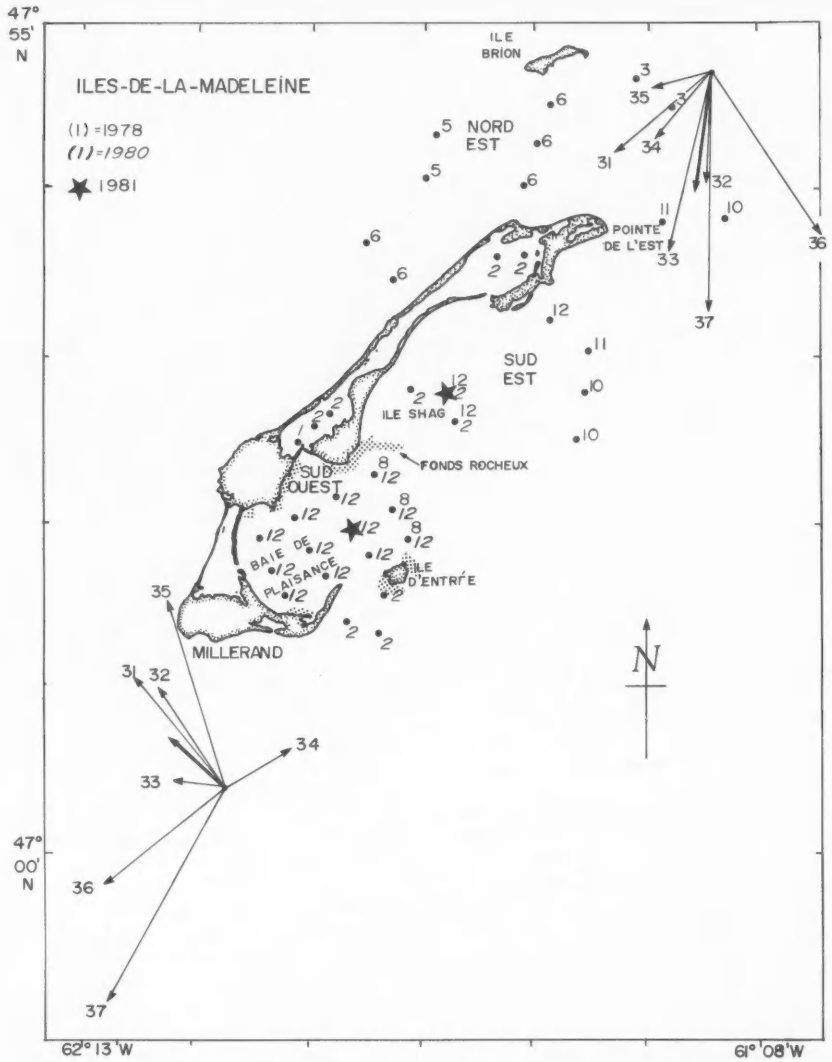


FIG. 1. Répartition des stations d'échantillonnage de larves de homard et nombre de traits de filets à plancton au cours des études de 1978 (Anonyme 1978a), 1980 et 1981. La localisation des deux courantomètres mouillés de juillet à septembre 1985 est aussi indiquée. La vitesse et la direction des courants résiduels moyens (flèche grasse) et hebdomadaires (flèches fines portant le numéro de la semaine) montrent le mouvement giratoire des eaux de surface ainsi que la variabilité temporelle de la direction du mouvement. Les fonds rocheux de la région de la baie de Plaisance (seulement) sont indiqués par les zones ombrées.

correspondent d'ailleurs très bien à ce modèle de circulation (Service de l'environnement atmosphérique 1984). Des travaux théoriques sur la circulation dans le golfe (Pingree et Griffiths 1980) prédisent de plus l'existence d'une petite zone de front située à l'extrémité nord-est.

Tout récemment, le mouillage de deux courantomètres (Anderaa Corp.) dans la couche de surface (10 m), aux deux extrémités de l'archipel, du 1er août au 16 septembre 1985 (Hudon, données inédites), a confirmé l'existence d'un tourbillon anticyclonique autour des îles de la Madeleine (fig. 1). Pour l'ensemble de la période de mouillage, la direction du courant résiduel moyen (flèches grasses) était vers le sud-est au large de la pointe de l'Est et vers le nord-ouest au large de Millerand. Cependant, la variabilité hebdomadaire (flèches fines numérotées) en direction était beaucoup plus élevée au sud de l'archipel, allant du nord-est (semaine 34) au sud-ouest (semaine 37).

Les îles étant situées au centre d'un vaste plateau côtier, l'action du vent en condition de faible profondeur a une forte influence sur la circulation (Lauzier 1952; Blackford 1978). La localisation de l'archipel et la configuration de ses côtes font que la face nord est exposée sur un angle de plus de 180°,

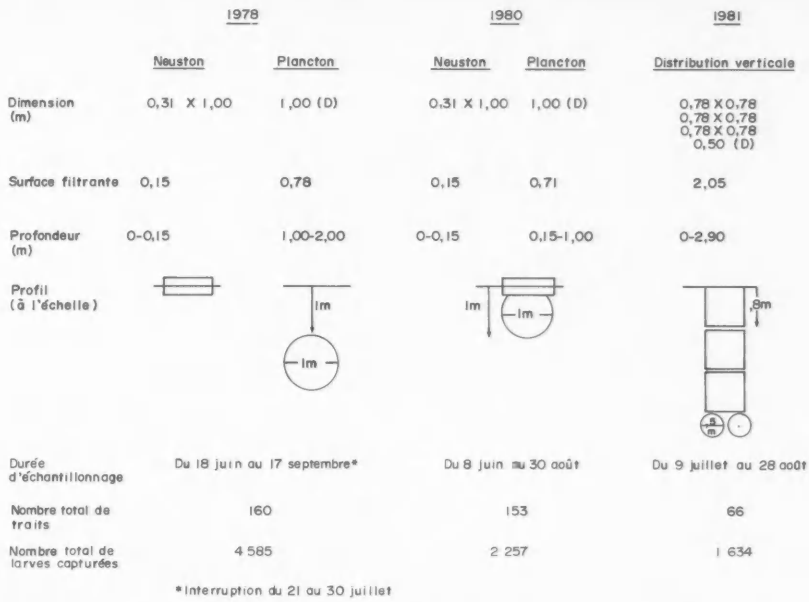


FIG. 2. Comparaison des engins d'échantillonnage et des efforts déployés pour évaluer l'abondance des larves de homards lors des trois saisons d'études. (*D*) = diamètre du filet.

angle de plus de 180°, occasionnant des fetches allant de 140 km vers l'île du Prince Édouard à 270 km vers le nord-est du golfe. Par ailleurs, la face sud est exposée sur moins de 135°, subissant un fetch de 100 km vers le Cap-Breton à 150 km vers Terre-Neuve (Ouellet 1977). La baie de Plaisance est particulièrement bien protégée, n'étant sensible qu'aux vents du nord-est.

Les vitesses moyennes et directions des vents de 1951 à 1980 (Service de l'environnement atmosphérique 1983) montrent la prédominance des vents du sud-ouest de juin à août, ce qui concorde avec les observations sur les courants de surface. Une étude du transport de sédiments littoraux dans la région nord-est des îles attribuait d'ailleurs aux vents (et aux vagues) le déplacement net observé vers l'est (Ouellet 1977).

Le temps de rétention plus élevé des eaux sur la face sud des îles, ainsi que la plus grande superficie des zones peu profondes dans ce secteur, s'expriment par des régimes thermiques différents sur les deux faces des îles (Lauzier *et al.* 1957). En été, période où la couche de mélange de surface est la plus mince (10–20 m) (Lauzier *et al.* 1957), l'évolution des températures de surface est sensiblement la même au nord et au sud des îles (Anonyme 1978a; Hudon et Fradette 1985). On note cependant que les températures de fond subissent une augmentation estivale plus rapide sur la face sud (Lauzier 1957) et en particulier dans la baie de Plaisance (Dobson et Pétrie 1984).

Ces caractéristiques hydrographiques particulières ont des conséquences très importantes sur la biologie du homard aux îles de la Madeleine. Ainsi, des travaux récents montrent que l'on peut diviser la population de homards des faces nord et sud des îles de la Madeleine en deux sous-unités ayant des caractéristiques biologiques distinctes. Les homards de la face nord ont une taille moyenne plus élevée (Bergeron 1967); la maturité sexuelle est atteinte à une taille supérieure (Dubé et Grondin 1985); la ponte et l'éclosion sont plus tardives (Axelsen et Dubé 1978; Attard et Fradette 1985) et les prises par unités d'effort augmentent plus lentement au cours de la saison de pêche sur la face nord que sur la face sud (Lamoureux *et al.* 1983). De plus, les études de marquage suggèrent que les homards n'effectuent pas de migrations d'une face des îles à l'autre (Dubé 1984), ce qui représente un facteur d'isolation supplémentaire. Les échanges entre les deux populations pourraient donc reposer principalement sur la dérive larvaire, ce qui permet aussi de supposer que les populations des faces nord et sud sont aussi soumises à des contraintes différentes au niveau du recrutement.

## Matériel et méthodes

La localisation géographique et le nombre d'échantillons pris à chacune des stations au cours des trois saisons sont indiqués à la figure 1. En 1978, les 17 stations étaient réparties autour de l'extrémité est des îles, alors qu'en 1980, les efforts se sont concentrés sur la baie de Plaisance (12 stations), l'île d'Entrée (3), l'île Shag (2) et les lagunes de Grande-Entrée (2) et de Havre-aux-Maisons (3). Cinq stations adjacentes de la région sud (île Shag et rangée est de la grille de stations de la baie de Plaisance) ont été échantillonnées en 1978 et 1980. L'échantillonnage de 1981 a été concentré aux deux stations où le plus grand nombre de larves avaient été récoltées en 1980, pour étudier plus en détail la répartition verticale des larves.

Le type d'engin utilisé, les périodes d'échantillonnage et le nombre de traits totaux sont présentés à la figure 2 pour les trois saisons d'échantillonnage. Les études de 1978 et de 1980 sur la répartition horizontale des larves utilisaient des engins similaires échantillonnant la couche de surface jusqu'à environ 1 m de profondeur. En 1981, la répartition verticale des larves a été étudiée au moyen d'un filet rectangulaire à trois compartiments superposés (fig. 3), du même type que celui utilisé par Harding *et al.* (1982), mais de plus grande taille. Pour les trois saisons, l'échantillonnage a été réalisé à intervalle hebdomadaire du

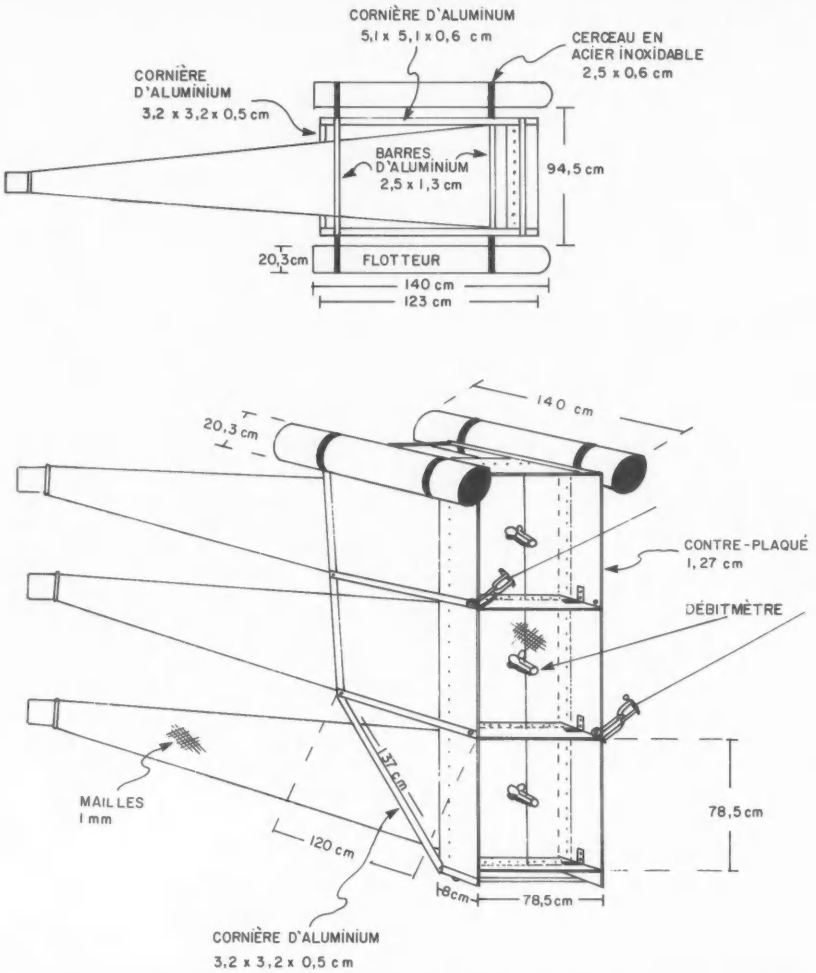


FIG. 3. Plan détaillé du filet à trois compartiments superposés utilisé pour l'échantillonnage des larves de homards à différentes profondeurs depuis la surface.

début de juin à la fin d'août, avec cependant en 1978, une interruption de 10 jours à la fin de juillet. L'effort consacré à l'étude de la répartition horizontale est de 160 traits en 1978 et de 153 en 1980.

À chaque échantillonnage, on a procédé à des mesures de température et de salinité (de surface), de transparence (disque de Secchi) et à une estimation de la nébulosité. En 1981, l'intensité lumineuse à la surface était obtenue soit par mesure directe avec un irradiomètre, soit par l'utilisation d'observations réalisées à la station météorologique de Cap-aux-Meules, ces dernières valeurs étant corrigées en utilisant l'estimation des paramètres à partir des tables du Smithsonian Meteorological Service (1971). On effectuait de plus une correction pour la nébulosité locale. L'état de la mer et l'abondance de débris flottant à la surface étaient aussi pris en note.

Pour les trois saisons, des traits de 30 minutes étaient faits avec les filets immergés sur le côté du bateau pour éviter que le reflux de l'eau causé par le navire n'interfère avec la récolte des larves. Les larves de homard ainsi récoltées étaient triées et leur stade de croissance identifié. Les valeurs mesurées par le débitmètre à chaque trait de filet permettaient de convertir les captures en densité de larves par kilomètre carré pour la couche supérieure de 1 m. Pour les données de 1978, ce calcul a été fait en retournant aux données originales de l'étude d'Anonyme (1978a).

Les résultats permettent de calculer, pour chaque secteur, la production et la survie des larves au cours de l'été. La production a été calculée par la méthode de Scarratt (1964), en tenant compte du temps mis par une larve de chacun des stades pour atteindre le stade suivant selon la température à laquelle elle est récoltée, évaluée par la méthode de Templeman (1936). La durée du stade IV est cependant inférieure à la période nécessaire à sa métamorphose en individu de stade V, puisque sa vie benthique pourrait débuter dès la moitié du stade IV (désigné par IV$\frac{1}{2}$ au tableau 1) (Scarratt 1973). La valeur de survie, calculée comme le pourcentage des individus produits au stade I ayant été récoltés au stade IV, tient compte de la durée de vie planctonique.

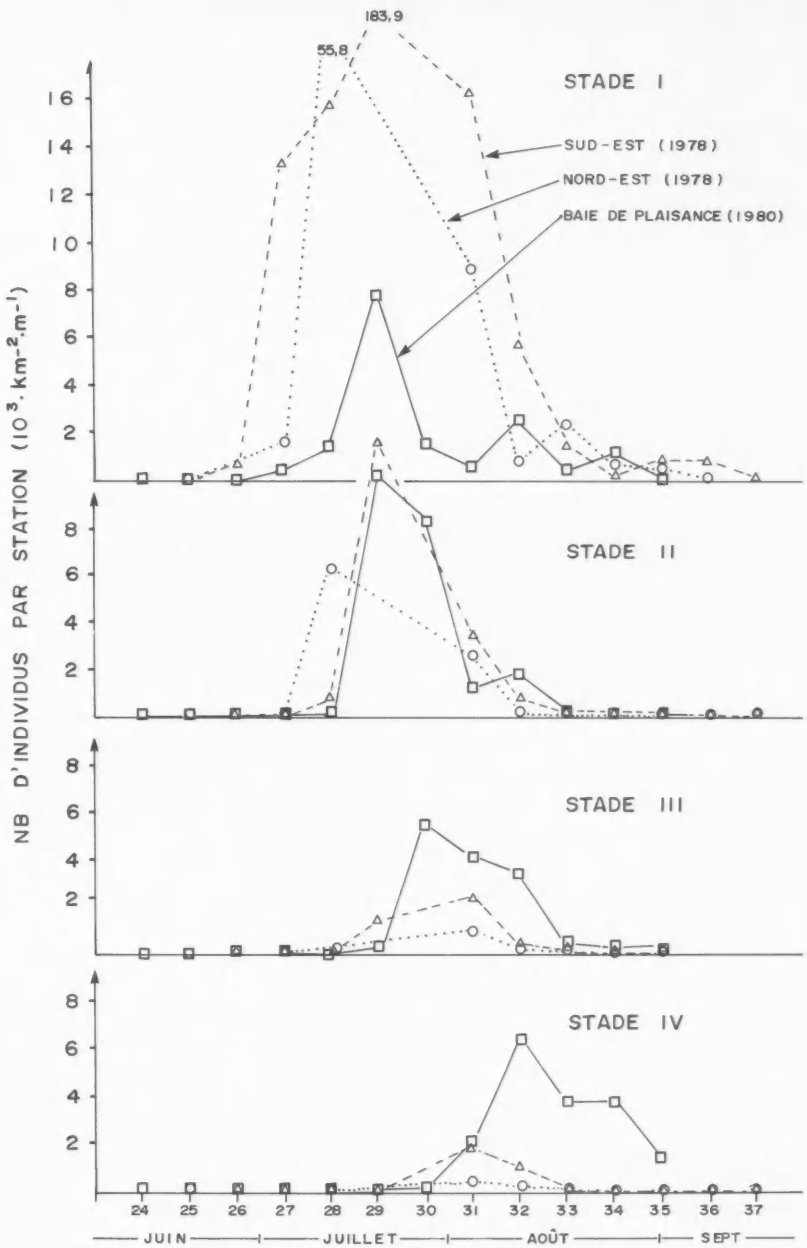


FIG. 4. Évolution saisonnière de l'abondance moyenne par station échantillonnée des quatre stades larvaires prélevés dans les secteurs nord-est, sud-est et sud-ouest (baie de Plaisance). Les secteurs nord-est et sud-est sont d'importants sites de production de larves de stade I mais recèlent de très faibles densités de larves des stades avancés. La baie de Plaisance produit peu de larves de stade I mais représente le site d'accumulation de larves de stade IV produites dans les autres secteurs.

Les données de la grille de 3 sur 4 stations dans la baie de Plaisance en 1980 furent utilisées pour étudier le schéma de répartition des larves pour la somme des densités observées au cours des 6 sem où des larves de stade IV ont été récoltées. Le type de relation existant entre la densité de larves, la distance à la côte et la distance aux fonds rocheux propices à la vie benthique a d'abord été examiné par les corrélations partielles. L'existence de gradients de facteurs physiques permettant aux larves de s'orienter vers les fonds propices a ensuite été examinée au moyen de corrélations simples de Pearson ($r$) avec la

température, la transparence (disque de Secchi) et la densité de débris de zostère. Cliff et Ord (1981) montrent cependant que le test de signification des corrélations n'est pas valide en présence d'autocorrélation spatiale dans les données, puisque le risque d'erreur de type I est accru (c.-à-d. qu'il y a risque de trouver une relation alors qu'elle est absente). Par conséquent, les tests de signification des corrélations ont été réalisés par permutation (« randomization test » : Sokal et Rohlf 1981); voir l'annexe.

## Résultats

### Répartition spatio-temporelle des larves

Les fluctuations saisonnières d'abondance des quatre stades larvaires récoltés en 1978 et 1980 sont illustrées à la figure 4. Le détail des cartes de répartition pour chaque stade est disponible dans le travail de Hudon et Fradette (1985). On note tout d'abord un décalage des pics d'abondance d'un stade à l'autre, les larves de stade I étant toujours les premières à être observées, leur pic d'abondance étant plus précoce et plus important que celui des stades subséquents. Pour le stade I, les récoltes les plus abondantes se situent entre la 27$^{e}$ et la 31$^{e}$ sem, et sont particulièrement importantes dans les régions nord-est et sud-est. On observe un chevauchement des pics d'abondance des larves de stade I au nord-est et au sud-est, quoique le pic d'abondance au nord-est semble être de plus courte durée que celui du sud-est. L'absence de données pour les 29$^{e}$ et 30$^{e}$ sem de l'été 1978 empêche cependant de conclure quant à leur importance relative. Les récoltes de larves de stade I dans la baie de Plaisance en 1980 sont très inférieures à celles des deux autres secteurs en 1978. On observe deux pics d'abondance de larves de ce stade, qui ont lieu respectivement au cours de la 29$^{e}$ et de la 32$^{e}$ sem.

Les larves de stade II sont déjà beaucoup moins abondantes dans les régions nord-est et sud-est, apparaissant cependant 2 sem plus tôt dans la première région, où des concentrations importantes étaient observées près de l'île Brion. Au fur et à mesure que la saison se déroule, apparaissent les stades plus avancés. Comme dans le cas des larves de stade I, on voit un pic principal d'abondance, suivi d'un épaulement à la 32$^{e}$ sem.

Les stades III et IV sont cependant très peu abondants au nord-est et au sud-est, tandis qu'ils apparaissent plus tard, mais avec une abondance accrue dans la baie de Plaisance.

Aux trois stations au nord de la baie de Plaisance (île Shag), on observe une concentration de stade I plus élevée que celle de la baie de Plaisance durant la 29$^{e}$ sem. Cette période correspond d'ailleurs à l'abondance maximale des larves de stade I dans le milieu. L'abondance des stades II, III et IV était cependant comparable à celle de la baie elle-même. Au cours de la 32$^{e}$ sem, ces trois stations montraient des concentrations nettement plus élevées de stades I et II alors que la baie de Plaisance n'avait que de faibles concentrations. Le stade III était de concentration équivalente alors que le stade IV était plus abondant dans la baie.

La comparaison des densités de larves de chacun des stades récoltés aux stations échantillonnées en 1978 et en 1980 a montré l'absence de différence significative (test de $t$ pairé, $t$ = 0,49; $p > 0,6$ pour 23 degrés de liberté) entre les densités des 2 années à ces stations.

Aux trois stations au sud de l'île d'Entrée, l'abondance des stades I et IV était plus élevée que dans la baie au cours de la 29$^{e}$ sem, alors qu'elle était comparable pour les stades II et III.

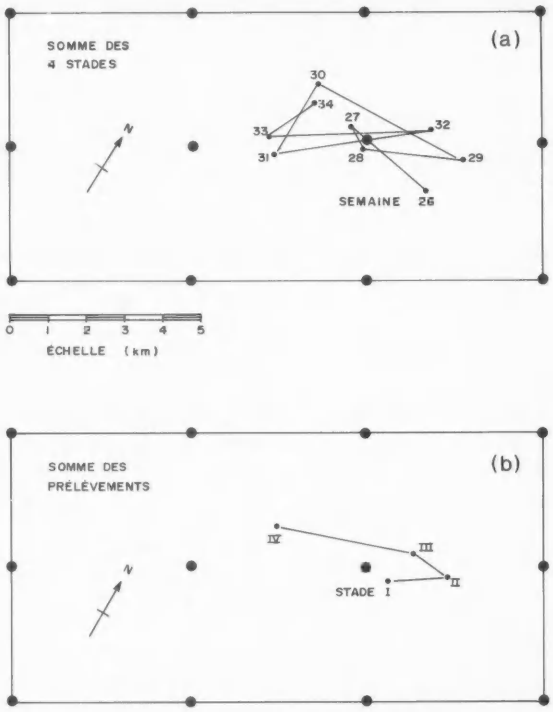


FIG. 5. (a) Déplacements du centre de masse des concentrations des quatre stades larvaires de homard groupés pour chaque semaine à l'intérieur de la baie de Plaisance en 1980. Pour l'ensemble des larves groupées, le centre de masse se déplace graduellement vers le fond de la baie en décrivant de larges boucles. (b) Déplacement du centre de masse de concentrations de chacun des stades larvaires à l'intérieur de la baie de Plaisance en 1980. Pour l'ensemble des prélèvements hebdomadaires, le centre de masse de chacun des stades est de plus en plus éloigné de l'entrée de la baie, le stade IV étant nettement séparé des trois premiers stades. La grille de 3 sur 4 points superposée au diagramme correspond aux 12 stations de la baie de Plaisance.

L'échantillonnage de ces stations à la 33$^{e}$ sem, après les pics d'abondance pour les trois premiers stades, montre des valeurs de densité comparables pour le stade IV seulement.

Dans les stations des lagunes de Grande-Entrée et de Havre-aux-Maisons, les larves de stades I, II et III étaient absentes dans les échantillons pris au cours des 31$^{e}$ et 32$^{e}$ sem. L'abondance du quatrième stade au cours de ces 2 sem était de 0,13 et 1,06 $\times$ $10^{3}$ ind. $\cdot$ km$^{-2}$ $\cdot$ m$^{-1}$, toujours inférieure à celle observée dans les stations côtières adjacentes (4,46 et 2,50 $\times$ $10^{3}$ ind. $\cdot$ km$^{-2}$ $\cdot$ m$^{-1}$, respectivement).

### Dispersion des larves dans la baie de Plaisance (sud-ouest)

L'échantillonnage hebdomadaire dans la baie de Plaisance permet de suivre les variations de la répartition des quatre stades. Les déplacements hebdomadaires du centre de masse de l'abondance totale des quatre stades (fig. 5a) forment des boucles alternant entre l'entrée et le centre de la baie. Cependant, le tracé du déplacement des centres de masse de chacun des stades (fig. 5b), pour l'ensemble des prélèvements hebdomadaires, montre que les trois premiers stades se concentrent surtout à l'entrée de la baie, tandis que le stade IV a son centre

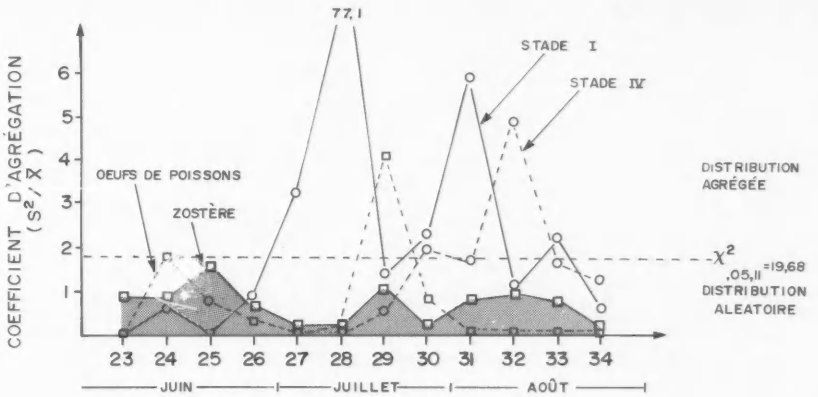


FIG. 6. Évolution saisonnière du coefficient d'agrégation (rapport variance/moyenne) des larves de stades I et IV, des débris de zostère et des oeufs de poissons prélevés simultanément à 12 stations dans la baie de Plaisance en 1980. La répartition des débris de zostère, qui est toujours non significativement différente d'une répartition au hasard, a été ombrée. La ligne pointillée sépare les éléments ayant une répartition aléatoire de ceux dont la répartition est agrégée d'après la valeur seuil du khi-carré. Les larves de stade I sont réparties de façon beaucoup plus irrégulière que les larves de stade IV et les oeufs de poisson.

TABLEAU 1. Corrélations paramétriques de Pearson ($r$, triangle supérieur) et corrélations partielles (triangle inférieur) entre la densité de larves de stade IV, la distance à la côte et la distance aux fonds rocheux. Les corrélations partielles montrent la relation entre chaque paire de variables après en avoir extrait l'influence de la troisième. Par exemple, la corrélation marginale entre la densité de larves et la distance à la côte ($-0{,}4518$, $p = 0{,}070$) disparaît totalement lorsqu'on en extrait l'influence de la distance aux fonds rocheux ($-0{,}0347$, $p = 0{,}460$); $p$ = niveau de probabilité de la corrélation. *Probabilité significative; **probabilité hautement significative.

| | Corrélations de Pearson ($r$) | | |
|---|---|---|---|
| | Larves de stade IV | Distance à la côte | Distance aux fonds rocheux |
| Larves de stade IV | 1 | $-0{,}4518$<br>$p = 0{,}070$ | $-0{,}6675$<br>$p = 0{,}009$** |
| Distance à la côte | $-0{,}0347$<br>$p = 0{,}460$ | 1 | $+0{,}6473$<br>$p = 0{,}011$* |
| Distance aux fonds rocheux | $-0{,}5516$<br>$p = 0{,}039$* | $+0{,}5205$<br>$p = 0{,}050$* | 1 |
| | Corrélations partielles | | |

de masse beaucoup plus loin vers l'intérieur. L'examen du déplacement hebdomadaire du centre de masse de chacun des stades pris individuellement indique que les déplacements des stades I, II et III s'effectuent dans la même direction, alors qu'on observe des divergences pour le stade IV.

Pour comprendre davantage la dispersion des différents stades larvaires, on a calculé leur coefficient d'agrégation (Elliott 1977) au cours de la saison. L'évolution saisonnière de ce coefficient (fig. 6) montre que les larves de stade I sont très fortement agrégées, les valeurs du rapport variance–moyenne atteignant 77,1, tandis qu'il ne dépasse pas 4,8 pour le stade IV. Les tracés parallèles du coefficient d'agrégation de deux types de matériaux inertes récoltés simultanément, les débris de zostère (*Zostera marina*) et les oeufs de poissons font état d'une répartition beaucoup plus uniforme, s'approchant d'une répartition aléatoire (rapport variance–moyenne égal à 1) dans le cas de la zostère (fig. 6, partie ombrée). Pour $n - 1 = 11$ degrés de liberté, toutes les valeurs du rapport variance–moyenne égales ou supérieures a 1,8 sont associées à une valeur de khi-carré ($\chi^2 = (S^2/\bar{X})\,(n-1)$) suffisamment élevée pour rejeter l'hypothèse d'une répartition aléatoire (fig. 6, ligne horizontale).

Il existe une forte corrélation négative ($r = -0{,}6675$, $p = 0{,}009$) entre la densité totale de larves de stade IV et la distance aux fonds rocheux où la métamorphose benthique s'effectue, tandis qu'il n'y a qu'une relation marginale entre la densité de larves de stade IV et la distance à la côte la plus proche ($r = -0{,}4518$, $p = 0{,}070$) (tableau 1, triangle supérieur). Les larves semblent donc se diriger vers les fonds rocheux qui leur sont favorables, et non vers n'importe quelle côte. Ceci est vérifié par la persistance de la corrélation entre la densité de larves et la distance aux fonds rocheux lorsqu'on enlève l'influence de la distance à la côte. Par contre, toute relation entre la densité des larves et la distance à la côte disparaît lorsque l'effet de la distance aux fonds rocheux est éliminé (tableau 1, triangle inférieur). Le modèle causal expliquant le mieux la relation entre ces trois variables serait donc du type suivant:

Distance à la côte ↔ Distance aux fonds rocheux → Densité de larves de stade IV

Pour déterminer si un gradient physique quelconque peut être utilisé pour l'orientation des mouvements des larves vers les fonds rocheux, nous avons calculé la corrélation entre la transparence, la température et la quantité de débris de zostère avec la distance aux fonds rocheux. Aucune relation significative n'a été obtenue pour chacun de ces trois facteurs physiques et la distance aux fonds rocheux, quoiqu'il existe un gradient positif de transparence avec la distance à la côte ($r = 0{,}6031$, $p = 0{,}024$). Ceci indique que, bien que les eaux deviennent moins transparentes à l'approche du littoral, le gradient de turbidité est d'une faible utilité pour guider les larves spéci-

TABLEAU 2. Comparaison des valeurs de production et de survie larvaires observées à différents endroits aux îles de la Madeleine et dans le golfe du Saint-Laurent. Les valeurs de production provenant des études de Scarratt (1964, 1973) et de Harding *et al.* (1982) ont été modifiées pour correspondre à un seul type d'unité (nombre de larves $\times 10^3 \cdot km^{-2} \cdot m^{-1}$). La production du stade IV½ est calculée d'après une estimation de la durée de vie planctonique égale à la moitié de la durée totale du stade IV (Scarratt 1973). En comparaison avec les travaux antérieurs, les valeurs en % de survie enregistrées aux îles de la Madeleine sont très basses au nord-est et au sud-est et exceptionnellement élevées dans la baie de Plaisance.

| Année | 1978 | | 1980 | 1949-1961 | 1962-1963 | | 1978 |
|---|---|---|---|---|---|---|---|
| Site | Îles de la Madeleine | | | Détroit de Northumberland | | | Baie Saint-Georges |
| | Nord-est | Sud-est | Baie de Plaisance | | | | |
| Référence | Cette étude modifiée d'après Anonyme (1978a) | | Cette étude | Scarratt[a] (1964) | Scarratt[b] (1973) | | Harding *et al.*[c] (1982) |
| Production | | | | | | | |
| Stade I | 103,2 | 280,1 | 18,2 | 367,4 | 149,9 | 338,1 | 407,8 |
| II | 7,8 | 10,9 | 13,9 | 54,1 | 11,4 | 27,3 | 132,2 |
| III | 0,6 | 1,2 | 5,8 | 13,3 | 2,4 | 4,3 | 35,6 |
| IV | — | — | — | 4,1 | — | — | — |
| IV½ | 0,2 | 1,4 | 5,8 | — | 0,2 | 0,5 | 10,0 |
| Nombre des stations | 1–9 | 1–9 | 12 | 23 | 15 | 15 | 13 |
| Durée (nombre de semaines) | 11 | 11 | 12 | ≃18 | ≃18 | ≃18 | 14 |
| Survie I–IV½ | 0,2 % | 0,5 % | 31,9 % | 1,12 % (0,17–2,49 %) | 0,11 % | 0,13 % | 2,45 % |

[a]Valeur moyenne pour 13 années transformée par unité de $km^2$ à partir d'une estimation du volume filtré par trait de 2 058 $m^3$ = 0,60 m × 3 430 $m^2$.
[b]Valeur annuelle transformée par unité de ($km^2$ × m) à partir d'une estimation du volume filtré par trait de 2 058 $m^3$.
[c]Valeur totale de production transformée en nombre × $10^3$ unités de $km^2$ à partir d'une estimation de la surface de la baie égale à 900 $km^2$.

fiquement vers les fonds rocheux favorables, qui ne représentent qu'une faible proportion de la superficie côtière totale.

## Production et survie

Les valeurs de production du stade I sont beaucoup plus élevées au nord-est et au sud-est que dans la baie de Plaisance (tableau 2). Il est à noter que les valeurs calculées pour 1978 sous-estiment principalement la production des premiers stades, en raison d'une interruption de l'échantillonnage pendant 10 jours. Cependant, la production des stades III et IV diminue de façon draconienne dans les deux premières régions tandis qu'elle reste relativement élevée dans la baie de Plaisance. La différence est la plus marquée au niveau du stade IV, qui est récolté en plus grande abondance dans la baie de Plaisance.

La comparaison de ces valeurs avec celles obtenues dans des études antérieures dans le golfe du Saint-Laurent montre que, bien que la production observée en 1978 au nord-est et au sud-est soit comparable aux autres régions, les valeurs de survie sont très faibles (tableau 2). D'autre part, la production dans la baie de Plaisance est très faible mais la survie y est exceptionnellement élevée (31,9 %) par comparaison avec les maxima observés dans d'autres régions (2,45 %).

## Répartition verticale des larves

Le tracé des variations de concentration des larves de chaque stade capturées aux différentes heures du jour (fig. 7) montre que les plus fortes proportions de stade I en surface surviennent de 15 h à 18 h et de 3 h à 6 h, soit en fin de journée et à l'aube. Par contre, plus de la moitié des larves de stade I se trouve à plus de 0,8 m de profondeur entre 9 h et 15 h et entre 21 h et 24 h, soit durant les périodes de forte luminosité et durant la nuit. Les fluctuations de la répartition verticale du stade I suggèrent de plus que ces migrations verticales semi-diurnes sont restreintes aux 2,5 m supérieurs, puisque seul un faible nombre de larves a été prélevé dans la couche la plus profonde échantillonnée, de 2,4 à 2,9 m.

Les stades subséquents montrent de moins en moins de variation de répartition verticale, les individus ayant tendance à se concentrer à la surface en tout temps, sauf pour les périodes de 12 h à 15 h et de 21 h à 24 h, où l'on observe une légère migration en profondeur.

Ces données nous permettent d'évaluer le facteur de correction nécessaire pour calculer les densités réelles dans toute la colonne d'eau échantillonnée (de 0 à 2,4 m) en calculant la proportion de larves de chaque stade présentes aux différentes profondeurs selon deux groupes d'intensité lumineuse ambiante (fig. 8). Le regroupement des intensités lumineuses a été restreint aux périodes correspondant au plein jour (valeurs > 13 $mW \cdot cm^{-2}$) ou aux faibles intensités lumineuses (valeurs < 13 $mW \cdot cm^{-2}$), en raison du petit nombre de larves et de prélèvements au cours de certaines périodes.

Aux intensités lumineuses inférieures à 13 $mW \cdot cm^{-2}$, seulement 34 % des larves de stade I sont à plus de 0,8 m de profondeur, et cette proportion diminue à mesure que le développement avance. Aux intensités lumineuses supérieures à 13 $mW \cdot cm^{-2}$, les larves de tous les stades semblent se répartir en profondeur (1–12 m), avec 73, 43, 41 et 22 % des larves de stade I, II, III et IV respectivement à plus de 0,8 m. Il semble

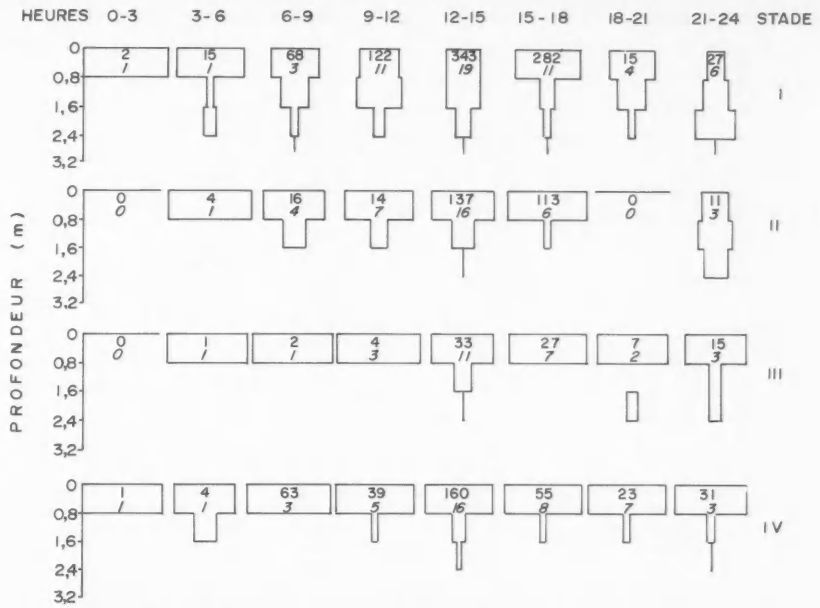


FIG. 7. Répartition verticale (de la surface à 2,9 m) des quatre stades larvaires selon l'heure d'échantillonnage, pour tous les traits de filets effectués en été 1981. Pour chaque profil vertical, le nombre de larves récoltées et le nombre de traits de filets dans lesquels les larves ont été prélevées (chiffres en italique) ont été indiqués. Les larves de stade I effectuent des migrations verticales nettes, nageant vers la surface à l'aube et au crépuscule. Avec l'âge, les larves sont de plus en plus concentrées près de la surface.

cependant que l'échantillonnage de la couche de surface sous-estime de moins en moins la densité à mesure que le stade larvaire progresse, avec la meilleure efficacité en faible intensité lumineuse.

## Discussion

Le bilan des entrées (naissance et immigration) et des sorties (mortalité et exportation) des larves dans un secteur donné permet d'évaluer leur taux de disparition. Par ailleurs, la différence entre l'immigration et l'exportation permet d'évaluer la rétention. Si l'on considère que le taux de mortalité des larves est le même pour les différents secteurs, le taux de « survie » tel que mesuré permet d'évaluer la rétention. Selon cette hypothèse, l'intégration du schéma de répartition spatio-temporelle autour des îles de la Madeleine suggère que la rétention des larves est de plus en plus prononcée en passant par les secteurs nord-est, sud-est et sud-ouest (baie de Plaisance). Cette hypothèse est confirmée par la configuration de la circulation des eaux de surface obtenue par le mouillage de courantomètres à l'été 1985.

### Secteurs de production d'oeufs et de larves

Les aires principales de production d'oeufs sont localisées à Grosse Île (nord-est) et à La Cormorandière (sud-est) (Attard et Fradette 1985). Ces zones correspondent aussi aux secteurs de plus forte production du premier stade larvaire (tableau 2), dont les pics d'abondance sont d'ailleurs légèrement décalés dans le temps. Les larves produites sur la face nord-est sont plus exportées que celles des autres secteurs, ce qui se reflète dans la très faible abondance des stades III et IV dans cette région (fig. 4). Sur la face sud-est, les larves produites localement s'ajoutent à celles transportées depuis la face nord, mais tout comme dans la région nord-est, le transport plus loin vers le sud contribue à réduire la densité des stades avancés. Ce transport s'exprime aussi par la plus longue durée de la période d'abondance de larves de stade I au sud-est (fig. 4).

Par contre, la baie de Plaisance contribue faiblement à la production d'oeufs, peut-être en raison de la faible superficie de fonds rocheux (Dubé 1984) et de la prédominance des prérecrues (Bergeron 1967) dans cette région. Malgré sa faible contribution au niveau de la production d'oeufs, cette région apparaît comme une zone importante de dépôt de larves passant de la phase planctonique à la phase benthique.

Le développement précoce des oeufs des femelles de la baie de Plaisance, lié aux températures de fond plus élevées (Templeman 1936), pourrait expliquer l'apparition précoce, en faible densité toutefois, de larves de stades I dès la mi-juin (24$^{e}$ sem) dans la baie (Hudon et Fradette 1985). Si on la compare aux valeurs des autres régions, la production locale de larves de stade I dans la baie de Plaisance est faible. L'apport de larves de l'extérieur explique donc les valeurs très élevées du « survie » (tableau 2). L'exportation des larves d'une région à l'autre serait donc la cause des différences extrêmes observées entre les valeurs de « survie » pour chacune des régions.

Les fluctuations d'abondance estivales du stade I dans la baie de Plaisance (fig. 4) montrent de plus deux pics d'abondance, le plus important ayant lieu à la mi-juillet (29$^{e}$ sem), suivi d'un pic secondaire 3 sem plus tard. Ces deux pics semblent se reproduire un peu plus tard dans la saison pour les stades II, III et IV et pourraient correspondre aux deux périodes d'éclosion

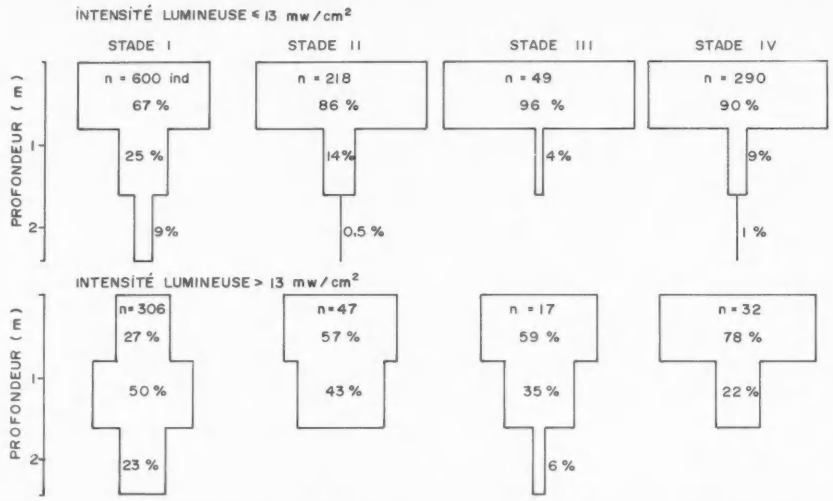


FIG. 8. Répartition verticale (de la surface à 2,4 m) des quatre stades larvaires selon l'intensité lumineuse mesurée lors de l'échantillonnage de l'été 1981. Pour chaque profil vertical, le nombre total de larves (*n*) et le pourcentage dans chaque intervalle de 0,8 m ont été indiqués. L'échantillonnage de surface sous-estime de moins en moins la densité à mesure que la stade larvaire avance, avec la meilleure efficacité à faible intensité lumineuse.

des oeufs rapportées par Attard et Fradette (1985). La présence de deux modes dans le développement des oeufs, se reflétant également au niveau de l'émergence des larves, suggère la présence de deux cohortes. Des travaux présentement en cours (Attard et Hudon, en préparation) examinent l'importance de ce phénomène de manière plus systématique.

### Stations périphériques et lagunaires

La validité du modèle de transport horizontal des larves est corroborée par les résultats provenant de l'échantillonnage des stations lagunaires et périphériques en 1980. L'abondance des stades I et II aux stations de l'île Shag suggère en effet un transport de jeunes larves vers le sud, où elles atteignent le stade IV. Dans le cas des stations de l'île d'Entrée, le schéma d'abondance pourrait être expliqué par l'effet conjugué de la production locale de larves et de l'apport de larves provenant soit de la baie de Plaisance, soit de la face nord-ouest de l'archipel. Bien que de bonnes concentrations de femelles ovigères aient été observées aux abords de l'île d'Entrée (Hudon, données inédites), le petit nombre de prélèvements empêche de tirer des conclusions plus précises quant à l'origine de ces larves. Cependant, les courants enregistrés au large de Millerand en 1985 indiquent que les larves de stade I produites au sud de l'île d'Entrée peuvent contribuer au recrutement de l'une ou de l'autre face des îles, selon la direction du courant prévalant lors de l'éclosion. Par exemple, un larve éclose durant la 34e sem serait restée du coté sud-est, tandis qu'elle aurait été transportée vers la face nord-ouest une semaine plus tard. Cette configuration de courants assure le mélange des populations de homards des deux faces des îles à l'étape du développement larvaire tout en permettant la rétention des larves dans les eaux côtières, ce qui confirme l'hypothèse selon laquelle les îles de la Madeleine constituent une cellule de recrutement indépendante (Dadswell 1979).

Dans les lagunes, l'absence de larves des stades I, II, III, mais la présence du stade IV est conforme aux résultats de Munro et Therriault (1983), montrant la quasi-absence de femelles ovigères à l'intérieur des lagunes, ce qui suggère que les larves y sont principalement transportées par les courants.

### Distribution horizontale dans la baie de Plaisance

D'après les résultats précédents, le mouvement des eaux autour des îles de la Madeleine suffirait à expliquer le schéma général de distribution des larves et permettrait de comparer la contribution relative des différentes régions à la production totale. Cependant, l'examen des variations spatio-temporelles à l'intérieur d'une même région permet d'évaluer l'importance respective des différents mécanismes pouvant affecter la répartition des larves. Outre les courants, le comportement des larves pourrait intervenir dans le schéma de distribution à échelle fine, soit par des mouvements natatoires horizontaux actifs ou par la migration verticale dans des masses d'eau superposées (Caddy 1979).

Dans la baie de Plaisance, le schéma de dispersion hebdomadaire du centre de masse des quatre stades larvaires (fig. 5a) forme de larges boucles, suggérant que la dérive se fait sans direction nette. Par contre, la figure 5b montre que les trois premiers stades larvaires sont concentrés à l'entrée de la baie, alors que le dernier stade est distribué plutôt vers le fond de la baie. Ce schéma peut être explicable, au moins en partie, par l'effet de dilution des masses d'eau transportées du sud-est à mesure qu'elles se mélangent à l'eau de la baie. La dilution progressive expliquerait la dispersion de plus en plus grande des individus des stades plus avancés (fig. 6).

En raison de la faible profondeur dans la baie de Plaisance (profondeur maximale de 12 m au centre), les vents contribuent fortement aux variations des courants de surface et influent sur le mélange vertical des eaux. Par ailleurs, la répartition des particules inertes (zostère et oeufs de poissons, fig. 6), entraînées au gré des courants de surface, semble relativement

homogène en dépit de l'effet de concentration dû aux sources locales de ces matériaux. Il est à noter que les pics d'agrégation de ces différents matériaux ainsi que des larves de stades I et IV ne sont pas simultanés, ce qui suggère que leur répartition respective n'est pas régie par les mêmes phénomènes. Aucune relation n'a cependant été observée entre l'abondance relative des débris de zostère et la densité de larves à chaque station, tel que l'avaient supposé Harding *et al.* (1982). Toutefois, considérant que la concentration de larves dans les cellules de Langmuir est un phénomène observable à une échelle plus fine (de l'ordre du mètre) que celle de notre échantillonnage, cette possibilité ne peut être écartée définitivement.

La capacité natatoire accrue des individus de stade IV par rapport aux autres stades peut être invoquée comme facteur supplémentaire pour expliquer leur plus grande dispersion. Cependant, bien que les larves plus âgées aient une meilleure capacité natatoire, ce facteur ne peut être le seul responsable du schéma observé et agit sans doute en conjugaison avec les facteurs précédents.

Malgré l'absence d'un mécanisme évident pour expliquer les mouvements horizontaux des larves, il existe cependant une relation significative entre la proximité des larves de stade IV et les fonds rocheux sur lesquels le dépôt benthique a lieu. L'orientation des larves vers ces fonds ne semble pas reposer sur un gradient de température, de turbidité ou d'abondance de débris. Le gradient plus général d'augmentation de turbidité à l'approche de la côte pourrait avoir un effet positif indirect, en diminuant la visibilité des larves pour les prédateurs lors de leurs plongeons pour explorer le fond.

### Distribution verticale

En raison de la faible densité des larves de homard, la plupart des efforts d'échantillonnage se sont concentrés sur la couche de surface, allant jusqu'à environ 1 m de profondeur au maximum (Scarratt 1973; Harding *et al.* 1982). Ces travaux montrent que les larves des stades I et II se concentrent dans les 30 cm supérieurs, quoique la faible représentation des larves de stades III et IV ait empêché les autres chercheurs d'établir avec certitude leur répartition verticale. D'après nos résultats, les premiers stades exécutent des migrations verticales plus prononcées et sont, par conséquent, les plus susceptibles d'être sous-estimés par un échantillonnage restreint à la couche de surface. Ainsi, la production larvaire pour les années 1978 et 1980, corrigée en fonction de l'intensité lumineuse et de la répartition verticale au moment de la capture (telle que calculée à la figure 8), produirait des valeurs de survie de 0,8 % (nord-est, 1978), de 1,0 % (sud-est, 1978) et de 59,3 % (baie de Plaisance, 1980). La correction des valeurs de production en fonction de la répartition verticale vient donc accroître la différence de survie entre les régions en augmentant la production de larves de stade I au nord-est et au sud-est.

Nos résultats montrent de plus que les larves de stade I effectuent deux migrations par jour, remontant vers la surface à l'aube et à la fin de l'après-midi, ce qui suggère une attraction vers la surface en conditions de lumière diffuse, et une distribution plus en profondeur en conditions de lumière intense. Ceci concorde tout à fait avec les hypothèses de Templeman et Tibbo (1945) et les observations de Ennis (1975) en laboratoire quant à l'importance de l'intensité lumineuse pour les larves. De plus, nos résultats indiquent que l'attraction vers la surface pourrait être déclenchée par les changements rapides d'intensité lumineuse plutôt que par une intensité donnée.

Si, comme le suppose Caddy (1979), la migration verticale joue un rôle dans le déplacement horizontal des larves, le centre de masse du stade I, étant le seul groupe effectuant des migrations verticales appréciables, devrait être différent de celui des autres stades. Or, seul le stade IV a son centre de masse à l'intérieur de la baie, tandis que celui des trois premiers stades est à l'entrée de la baie. En conjuguant ces résultats à nos connaissances de la migration verticale, il semble que les migrations verticales jouent plutôt un rôle indirect dans la dispersion, en ralentissant la dilution des nuages de larves de stade I qui descendent périodiquement sous la couche de surface, où l'effet des courants induits par le vent est atténué. À mesure que le temps de résidence dans la couche de surface augmente, l'effet de dilution des courants de surface deviendrait progressivement plus prononcé, avec une augmentation marquée pour le stade IV, qui reste constamment à la surface. Au cours du quatrième stade larvaire, la larve exécute des plongeons vers le fond pour trouver un substrat rocheux favorable à son existence benthique (Bertran *et al.* 1985), ayant la capacité de retarder sa métamorphose au stade V lorsque le substrat n'est pas adéquat (Cobb 1968). Le déplacement marqué du centre de masse des larves de stades IV vers le fond de la baie, où se trouvent plusieurs fonds rocheux propices à la vie benthique, suggère que les larves peuvent s'orienter dans l'espace, peut-être en détectant chimiquement la présence d'individus de leur espèce ou de certaines composantes de la communauté benthique des fonds rocheux. Ces facultés ont été démontrées pour les larves de nombreuses espèces d'invertébrés marins (Chia et Rice 1978) et expliqueraient la grande sélectivité des larves de homard à l'égard de leur site de dépôt benthique.

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## Références

ANONYME. 1978a. Larves de homards. Aménagement portuaire Leslie, îles de la Madeleine, étude d'impact sur l'écosystème marin. Dossier d'étude D soumis au ministère des Transports, gouvernement du Québec.

1978b. Dériveurs de surface. Aménagement portuaire Leslie, îles de la Madeleine, étude d'impact sur l'écosystème marin. Dossier d'étude G soumis au ministère des Transport, gouvernement du Québec.

ATTARD, J. ET P. FRADETTE. 1985. Développement des oeufs et fécondité des femelles de homard (*Homarus americanus*) aux îles de la Madeleine, Québec. Doc. Rec. CSCPCA 85/15.

AXELSEN, F. ET P. DUBÉ. 1978. Étude comparative du homard (*Homarus americanus* Milne-Edwards) des différentes régions de pêche des îles de la Madeleine. Ministère de l'Industrie et du Commerce. Dir. gén. pêches marit. Cahier d'information 86 : 49 p.

BERGERON, J. 1967. Contribution à la biologie du homard (*Homarus americanus* M.-Edw.) des îles de la Madeleine. Nat. can. 94 : 169–207.

BERTRAN, R., J.-Y. GAUTHIER ET J. LOREC. 1985. Variations de la phase pélagique des post-larves de homard européen, *Homarus gammarus*, en fonction de la nature du fond. ICES, C.M. 1985/K : 22.

BLACKFORD, B. L. 1978. Wind-driven inertial currents in the Magdalen shallows, Gulf of St. Lawrence. J. Phys. Oceanogr. 8 : 653–664.

BUMPUS, D. F. ET L. M. LAUZIER. 1965. Surface circulation on the Continental Shelf off eastern North America between Newfoundland and Florida. Folio 7. *Dans* W. Webster [éd.] Serial atlas of the marine environment. Am. Geogr. Soc., New York, NY.

CADDY, J. F. 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the american lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 175 : 204–216.

CHIA, F. S. ET M. E. RICE [ÉD.]. 1978. Settlement and metamorphosis of marine invertebrate larvae. Elsevier, New York, NY. 290 p.

CLIFF, A. D. ET J. K. ORD. 1981. Spatial processes : models and applications. Pion Ltd., Londres. 266 p.

COBB, J. S. 1968. Delay of moult by the larvae of *Homarus americanus*. Ecology 52 : 108–115.

DADSWELL, M. H. 1979. A review of the decline in lobster (*Homarus americanus*) landings in Chedabucto Bay between 1956 and 1977 with an hypothesis for a possible effect by the Canso Causeway on the recruitment mechanism of eastern Nova Scotia lobster stocks. Can. Fish. Mar. Serv. Tech. Rep. Ser. 834 (Part 3) : 113–144.

DOBSON, D. ET B. PETRIE. 1984. Long-term temperature monitoring program 1983, Scotia–Fundy, Gulf regions. Can. Data Rep. Hydrogr. Ocean Sci. 22 : 406 p.

DUBÉ, P. 1984. Analyse des déplacements du homard (*Homarus americanus*) sur les côtes des îles de la Madeleine, à partir des données de marquage et de recapture, de 1978 à 1982. Doc. Rec. CSCPCA 84/57.

DUBÉ, P. ET P. GRONDIN. 1985. Maturité sexuelle du homard (*Homarus americanus*) femelle aux îles de la Madeleine. Doc. Rec. CSCPCA 85/85.

ELLIOTT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biol. Assoc. Sci. Publ. 25 : 157 p.

EL-SABH, M. I. 1976. Surface circulation pattern in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 33 : 124–138.

ENNIS, G. P. 1975. Behavioral responses to changes in hydrostatic pressure and light during larval development of the lobster (*Homarus americanus*). J. Fish. Res. Board Can. 32 : 271–281.

1983. The effect of wind direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland nearshore area. Can. Tech. Rep. Fish. Aquat. Sci. 1138 : 19 p.

FOGARTY, M. J. [ÉD.]. 1983. Distribution and relative abundance of american lobster, *Homarus americanus*, larvae : New England investigations during 1974–79. NOAA Tech. Rep. NMFS SSRF–775. 64 p.

HADLEY, P. B. 1908. The behavior of the larval and adolescent stages of the american lobster (*Homarus americanus*). J. Comp. Neurol. Psychol. 18 : 200–301.

HARDING, G. C., W. P. VASS ET K. DRINKWATER. 1982. Aspects of larval american lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia. Can. J. Fish. Aquat. Sci. 39 : 1117–1129.

HUDON, C. ET P. FRADETTE. 1985. Variation spatio-temporelle des larves de homard (*Homarus americanus*) des îles de la Madeleine, Québec. Doc. Rec. CSCPCA 85/23.

LAMOUREUX, P., P. DUBÉ, P.-E. LAFLEUR ET J. FRÉCHETTE. 1983. Problématique de l'échantillonnage du crabe des neiges (*Chionoecetes opilio*) et du homard (*Homarus americanus*) et analyse du système d'échantillonnage au Québec. Can. Spec. Publ. Fish. Aquat. Sci. 66 : 279–290.

LAUZIER, L. M. 1952. Effect of storms on the water conditions in the Magdalen shallows. J. Fish. Res. Board Can. 8 : 332–339.

1957. Bottom temperatures on the Magdalen shallows. Bull. Fish. Res. Board Can. 111 : 269–285.

LAUZIER, L. M., R. W. TRITES ET H. B. HACHEY. 1957. Some features of the surface layer of the Gulf of St. Lawrence. Bull. Fish. Res. Board Can. 111 : 195–212.

MUNRO, J. ET J.-C. THERRIAULT. 1983. Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des îles de la Madeleine. Can. J. Fish. Aquat. Sci. 40 : 905–918.

OUELLET, Y. 1977. Notes sur l'influence du transport littoral sur la construction d'un port pour minéraliers aux îles de la Madeleine. Rapport préliminaire GCT-77-01, soumis au ministère des Transports, gouvernement du Québec.

PINGREE, R. D. ET D. K. GRIFFITHS. 1980. A numerical model of the M2 tide in the Gulf of St. Lawrence. Oceanol. Acta 3 : 221–225.

POTTLE, R. A. ET R. W. ELNER. 1982. Substrate preference behavior of juvenile american lobster *Homarus americanus*, in gravel and silt clay sediments. Can. J. Fish. Aquat. Sci. 39 : 928–932.

SANSCHAGRIN, R. 1964. Les îles de la Madeleine. Rapport géologique 106. Ministère des richesses naturelles, Québec. 59 p.

SCARRATT, D. J. 1964. Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. J. Fish. Res. Board Can. 30 : 1819–1824.

1973. Abundance, survival, and vertical and diurnal distribution of lobster larvae in Northumberland Strait, 1962–63, and their relationships with commercial stocks. J. Fish. Res. Board Can. 30 : 1819–1824.

SCARRATT, D. J. ET G. E. RAINE. 1967. Avoidance of low salinity by newly hatched lobster larvae. J. Fish. Res. Board Can. 24 : 1403–1406.

SERVICE DE L'ENVIRONNEMENT ATMOSPHÉRIQUE. 1983. Normales climatiques au Canada. Tome 5. Environnement Canada, Ottawa (Ont.).

1984. Cartes de l'état des glaces. Centre de prévision des glaces, Environnement Canada, Ottawa (Ont.).

SMITHSONIAN METEOROLOGICAL SERVICE. 1971. Tables. Smithsonian Institute, New York, NY.

SOKAL, R. R. ET F. J. ROHLF. 1981. Biometry : The principle and practice of statistics in biological research. 2e éd. W. H. Freeman and Co., San Francisco, CA. 859 p.

STASKO, A. B. 1980. Lobster larval surveys in Canada. Can. Tech. Rep. Fish. Aquat. Sci. 932 : 157–165.

STASKO, A. B. ET D. J. GORDON. 1983. Distribution and relative abundance of lobster larvae off southwestern Nova-Scotia 1977–1978. Can. Tech. Rep. Fish. Aquat. Sci. 1175 : 23 p.

TEMPLEMAN, W. 1936. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J. Biol. Board Can. 2 : 485–497.

1937. Habits and distribution of larval lobsters (*Homarus americanus*). J. Biol. Board Can. 3 : 343–347.

1939. Investigations into the life history of the lobster (*Homarus americanus*) on the west coast of Newfoundland, 1938. Nfld. Dep. Nat. Res. Fish. Res. Bull. 7 : 52 p.

TEMPLEMAN, W. ET S. N. TIBBO. 1945. Lobster investigations in Newfoundland 1938–1941. Nfld. Dep. Nat. Res. Fish. Res. Bull. 16 : 98 p.

## Annexe. Le calcul du niveau de signification par permutations

Les tests par permutation requièrent beaucoup plus de calculs que les tests faisant référence aux distributions théoriques, quoiqu'ils présentent les avantages d'être toujours valides, qu'il y ait autocorrélation ou non. De plus, ils ne sont pas affectés par la petite taille des échantillons.

Les tests de permutation pour les corrélations suivent le principe général suivant. D'après $H_0$, il n'existe aucune relation entre les variables, de telle sorte que n'importe quelle combinaison de valeurs des deux variables aurait pu être observée dans n'importe lequel des échantillons. La distribution d'échantillonnage de chaque terme statistique à déterminer (ici, $r$, le coefficient de corrélation) est obtenue en permutant au hasard les valeurs de l'une des variables entre les échantillons. Après chacune des permutations, le coefficient de corrélation était recalculé. Après avoir effectué un grand nombre de permutations (250 ou 1 000), on reconstituait la distribution de fréquence des valeurs obtenues par calcul pour la comparer à celle des valeurs réellement obtenues lors de l'échantillonnage. Si les valeurs extrêmes obtenues par permutations étaient moins fréquentes que dans l'échantillonnage, selon un niveau de signification pré-sélectionné, l'hypothèse nulle était rejetée et la corrélation était déclarée significative.

# Swimming Ability of Larval American Lobsters, *Homarus americanus*, in Flowing Water

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Ennis, G. P. 1986. Swimming ability of larval American lobsters, *Homarus americanus*, in flowing water. Can. J. Fish. Aquat. Sci. 43: 2177–2183.

The swimming capacity of American lobster, *Homarus americanus*, larvae in flowing water was observed in a screened-off portion of a flow tank. At a flow rate of 2 $cm \cdot s^{-1}$, stage I–III larvae were swimming for 46–74% of the observations during the first 5 min but this ranged from 0 to 28% toward the end of a 30-min period. At higher flow rates, however, very few of these larvae were able to continue swimming longer than 5 min. Newly molted stage IV larvae displayed substantially improved swimming ability compared with earlier stages. At 2 $cm \cdot s^{-1}$, these larvae were swimming for 40–48% of the observations over the 30-min period, although at higher flow rates their capacity to continue swimming was also limited and few were observed swimming longer than 10 min. Older stage IV larvae were more capable swimmers than newly molted stage IV larvae and displayed a capacity to continue swimming over the 30-min observation period at flow rates up to 9 $cm \cdot s^{-1}$. In flowing water, the frequency of orientation in the upstream direction for larvae that were swimming was higher than for control larvae. For stage IV larvae especially, this frequency was higher at the higher flow rates. The observations demonstrate the presence of a rheotactic response in all larval stages of the American lobster. The response is relatively weak in stages I–III but strong in stage IV.

L'aptitude à la nage des larves de homard américain, *Homarus americanus*, dans l'eau courante a été observée dans un bassin à écoulement continu dont une partie avait été barrée par une grille. À une vitesse de 2 $cm \cdot s^{-1}$, les larves des stades I à III nageaient lors de 46 à 74 % des observations pendant les 5 premières minutes, mais ce pourcentage tombait à 0 à 28 % vers la fin d'une période de 30 min. Toutefois, à des vitesses supérieures, rares étaient les larves capables de continuer à nager pendant plus de 5 min. Les larves de stade IV ayant mué depuis peu manifestaient une aptitude à la nage nettement supérieure par rapport aux stades antérieurs. À 2 $cm \cdot s^{-1}$, ces larves nageaient lors de 40 à 48 % des observations pendant la période de 30 min, mais à des vitesses supérieures leur aptitude à continuer à nager était également limitée, et elles étaient rares à nager pendant plus de 10 min. Les larves de stade IV mais plus âgées étaient plus aptes à la nage que celles qui venaient de muer et réussissaient à continuer à nager pendant la période d'observation de 30 min à des vitesses pouvant aller jusqu'à 9 $cm \cdot s^{-1}$. En eau courante, la fréquence d'orientation vers l'aval des larves qui nageaient était supérieure à celle des larves témoins. Pour les larves de stade IV, particulièrement, cette fréquence était supérieure aux vitesses les plus élevées. Les observations démontrent la présence d'une réaction rhéotaxique à tous les stades larvaires du homard américain. Cette réaction est relativement faible aux stades I à III mais elle est forte au stade IV.

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Mechanisms that determine where American lobster, *Homarus americanus*, larvae that originate in a given area eventually settle are largely unknown. There is evidence that all larval stages are restricted in vertical distribution to very close to the surface (Phillips and Sastry 1980). Some authors (Dadswell 1979; Harding et al. 1983) argued that downstream transport of larvae by surface currents is the key mechanism of recruitment, distance transported depending on current velocity and the time required for larvae to develop to settling stage which is related to temperature. Others (Squires 1970; Caddy 1979) suggested that larvae move vertically to an extent that enables them to maintain position near parental grounds by means of countercurrents.

Various recruitment processes, in which behavioral responses of larvae to environmental stimuli such as gravity, light, salinity, and hydrostatic pressure are essential components of the mechanisms involved, have been proposed for a number of decapod crustacea (Phillips 1981; Sulkin 1984; Ennis 1983 for review). American lobster larvae respond to many stimuli (Phillips and Sastry 1980) and it is reasonable to assume that recruitment processes in this species involve larval behavior.

Water currents are important in decapod crustacean larval recruitment mechanism but there are few studies of behavioral responses of larvae to this stimulus. Puerulus larvae of the western rock lobster (*Panulirus longipes*) can maintain mean swimming speeds of 15 $cm \cdot s^{-1}$ while swimming against water currents of velocities from 9 to 13 $cm \cdot s^{-1}$ as they approach a light source (Phillips and Olsen 1975). These larvae appeared to be attracted by light and swam across as well as against the current. Whether rheotaxis (i.e. directed reaction to flowing

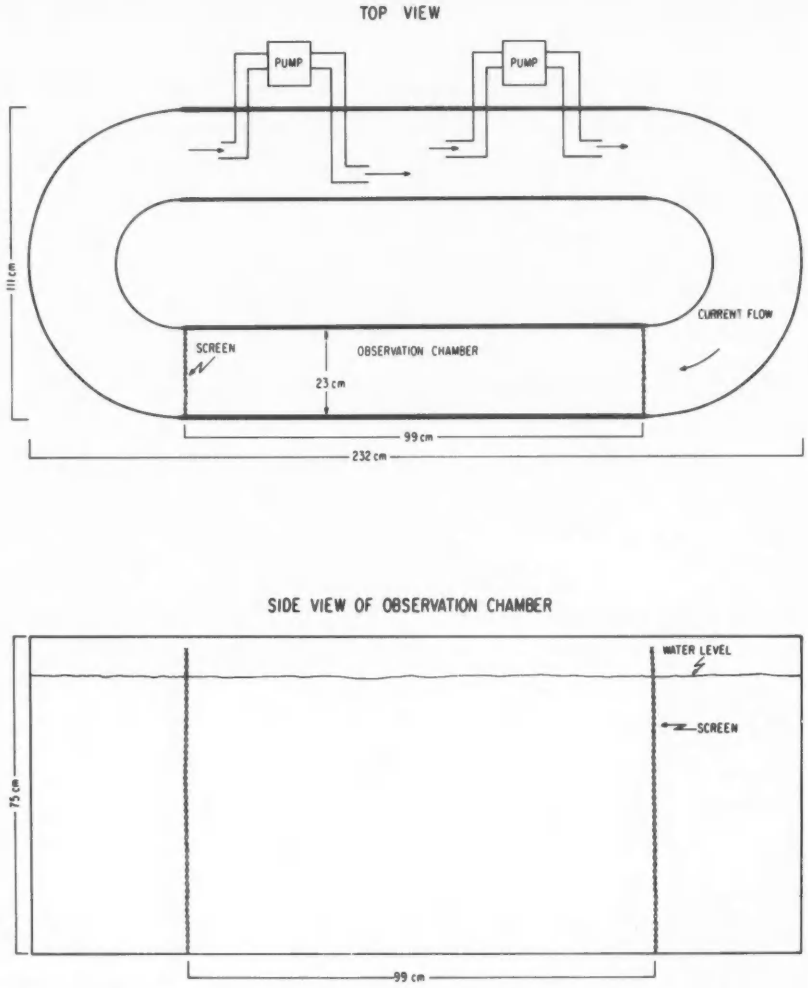


FIG. 1. Diagram of flow tank in which swimming of larval stages of *Homarus americanus* was observed.

water) contributed to their swimming is unclear. Prawn (*Macrobrachium rosenbergii*) larvae can swim against a water current of 0.8 $cm \cdot s^{-1}$ but this was due to positive phototaxis (Moller 1978). Hadley's (1906) study of rheotaxis appears to be the only attempt to determine the nature of behavioral responses of larval stages of the American lobster to water current. He made observations in large hatching/rearing containers in which strong circular currents were maintained by means of rotating paddles. He described swimming of the first three stages as being uncertain and desultory, although stage III larvae often displayed a tendency to retain equilibrium in the water. Immediately upon molting into stage IV, however, larvae headed into the current and swam against it. If the current was not too strong, they often made headway but in strong currents they were dispiaced. This response by stage IV larvae appeared to be more definite at night.

The present study was carried out to examine the rheotactic response of all larval stages of the American lobster over a range of current velocities to gain insight into the possible contribution of the response as a larval recruitment mechanism.

## Materials and Methods

Twelve ovigerous lobsters were obtained from Long Harbour, Placentia Bay, soon after removal from traps during late April – early May 1984. They were transported to the laboratory at St. John's, Nfld., and maintained in flowing seawater with ambient light. Temperature was increased gradually from 2°C and maintained at 12–14°C. When hatching was imminent, a lobster was held in a tank from which larvae could be collected soon after they hatched. Larvae were held in 53-cm-diameter by 57-cm-high containers with 1.3-mm plastic mesh bottoms which were positioned 6 cm off the bottom of larger tubs through which seawater flowed continuously. Dead larvae and debris were siphoned daily from the containers and *Artemia* nauplii were added to provide food in excess. Soon

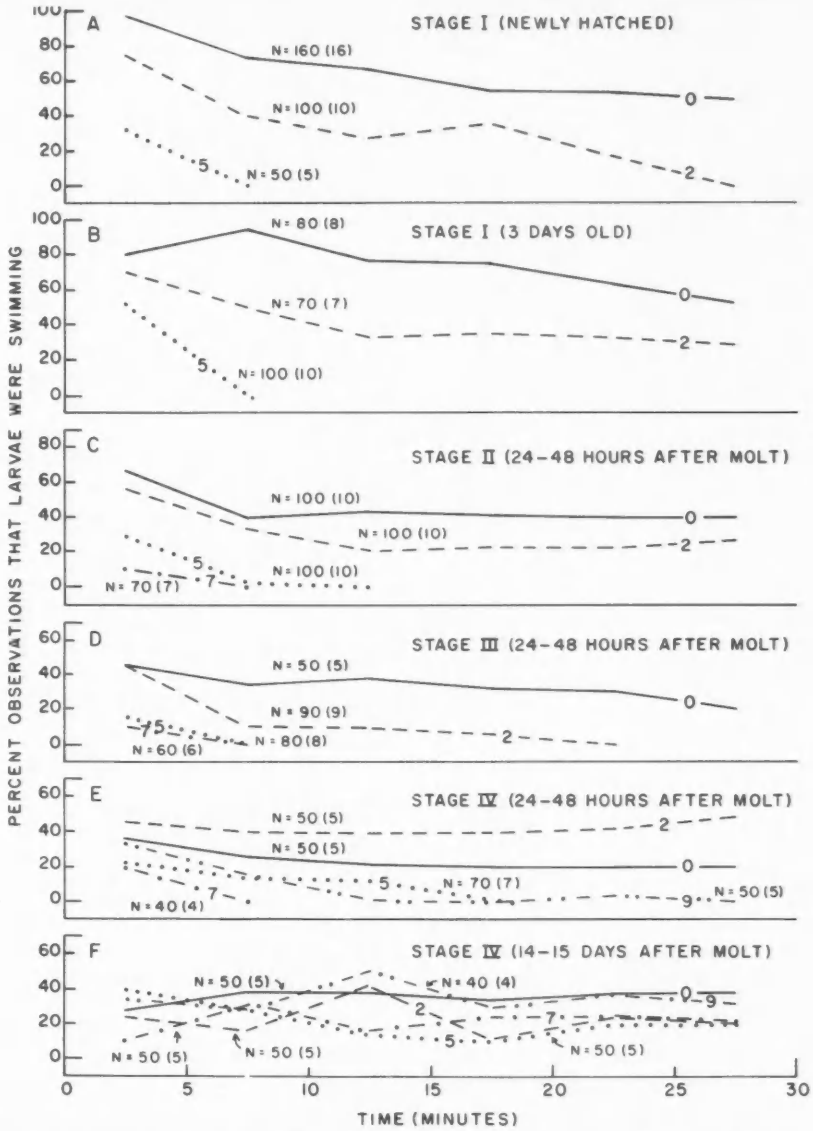


FIG. 2. Frequency of swimming in flowing water by larvae of *Homarus americanus*. For observations at 30-s intervals, percent in which larvae were swimming is presented for 5-min periods. Numbers in the lines are current velocities ($cm \cdot s^{-1}$); solid lines marked zero represent controls. $N$ = the number of observations, and in parentheses is the number of individual larvae observed.

after molting to stage III, larvae were held individually in 7-cm-diameter by 13-cm-high plastic cylinders with mesh bottoms positioned 5 cm off the bottom in vats through which seawater flowed continuously.

Swimming of individual larvae was observed in a Plexiglas chamber which formed one side of a flow tank (Fig. 1). A 1.3-mm plastic mesh screen was positioned at each end of the chamber to retain larvae. Two variable speed pumps maintained a flow of water through the chamber at velocities up to 11.5 $cm \cdot s^{-1}$. A fluorescent light fixture with two 118-cm-long tubes was positioned 104 cm above the observation chamber. This fixture was fitted with a black plastic skirt to minimize light scatter and to provide the only light during observations. Intakes for the pumps were positioned "upstream" and outlets "downstream" in the side of the tank opposite the observation chamber (Fig. 1). The outlet for each pump was two 20-cm-long by 18-mm-diameter pipes capped at the ends with 6-mm-diameter holes along one side. These pipes were positioned horizontally across the tank with holes oriented "downstream." Pump outputs were adjusted until the desired current velocity, measured at the surface, was achieved. The pumps were stopped to allow the water to become motionless

TABLE 1. Percent of observations in which stage IV larvae of *Homarus americanus* were mobile (i.e. swimming or crawling) in flowing water and percent of the observations of mobility that larvae were swimming.

| Flow rate ($cm \cdot s^{-1}$) | Stage IV (24–48 h after molt) | | Stage IV (14–15 d after molt) | |
|---|---|---|---|---|
| | % mobile ($N$)[a] | % swimming ($N$)[b] | % mobile ($N$)[a] | % swimming ($N$)[b] |
| Control | 82 (300) | 29 (247) | 84 (300) | 42 (252) |
| 2 | 77 (300) | 55 (231) | 75 (300) | 31 (225) |
| 5 | 12 (420) | 70 (50) | 49 (300) | 45 (146) |
| 7 | 3 (240) | 100 (8) | 64 (300) | 34 (191) |
| 9 | 24 (300) | 38 (73) | 70 (240) | 51 (168) |
| 11.5 | 2 (240) | 0 (4) | 88 (120) | 0 (106) |
| Total (2–11.5 $cm \cdot s^{-1}$) | 24 (1500) | 54 (336) | 66 (1260) | 34 (836) |

[a]$N$ = total number of observations.
[b]$N$ = number of observations in which larvae were mobile.

TABLE 2. Percent positive orientation for *Homarus americanus* larvae while swimming in flowing water. All observations ($N$) for 30-min period are combined.

| Stage | Flow rate ($cm \cdot s^{-1}$) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Control | | 2 | | 5 | | 7 | | 9 | |
| I (newly hatched) | 52 | (631) | 5 | (205) | 50 | (16) | | | | |
| I (3 d old) | 47 | (353) | 68[a] | (175) | 69[a] | (52) | | | | |
| II | 45 | (273) | 69[a] | (184) | 81 | (32) | 100 | (7) | | |
| III | 51 | (100) | 66 | (64) | 85 | (13) | 50 | (6) | | |
| IV (24–48 h after molt) | 47 | (72) | 49 | (128) | 83 | (35) | 88 | (8) | 89 | (28) |
| IV (14–15 d after molt) | 48 | (107) | 67[a] | (69) | 79[a] | (66) | 70[a] | (64) | 94[a] | (85) |

[a]Indicates that percentage is higher than for controls at $P = 0.05$ based on $\chi^2$ from a $2 \times 2$ contingency table.

before observations were initiated.

It would be very difficult to produce a uniform flow of water through a tank like the one used in this study. Velocity gradients near the water–tank interfaces cause turbulent flow (Vogel 1981) to which pump action would contribute. To make flow through the observation chamber of the flow tank as uniform as possible, pump intakes were positioned at 21 and 62 cm and outlets at 5, 25, 48, and 72 cm below the surface. The mesh screens probably helped to reduce turbulence. However, there was some turbulence throughout the observation chamber at all flow rates and velocity varied slightly at different positions. There was no indication, however, that the observations on swimming performance of larvae were affected by the non-uniform flow.

A larva was removed from its rearing container with a small, fine-meshed dipnet and placed at the surface in the center of the observation chamber; the pumps were started at the same time. Position of the larva was obtained by reference to an alphanumeric grid ($10 \times 10$ cm) marked around the edges of the observation chamber. Orientation of the larva (i.e. direction in the horizontal plane in which a swimming larva was headed) was assigned to one of four quadrants. The upstream and downstream quadrants (i.e. each ranging to 45° from the vertical plane parallel to the sides of the observation chamber) were considered positive and negative orientation, respectively. Position and orientation of the larva were recorded at 30-s intervals over a standard 30-min observation period. When a larva was held against the downstream screen by the flowing water (i.e. entrained) for more than 2 min, observations were terminated but it was assumed that the larva would have been entrained for the remainder of the observation period.

## Results

### Swimming Performance

In flowing water, the ability of larvae to remain swimming in the observation chamber and avoid entrainment on the downstream screen improved with larval development. At a flow rate of 2 $cm \cdot s^{-1}$, stage I–III larvae were swimming for 46–74% of the observations during the first 5 min but this percentage ranged from 0 to 28 during the last 5-min interval (Fig. 2A–2D). However, at higher flow rates there were very few observations of these larvae swimming beyond the first 5 min.

Newly molted stage IV larvae displayed substantially improved swimming ability compared with earlier stages. At 2 $cm \cdot s^{-1}$, these larvae were swimming for 40–48% of the observations over the 30-min period (Fig. 2E). At higher flow rates the capacity of these larvae to continue swimming was limited, but there were some observations of swimming beyond 10 min.

Older stage IV larvae were more capable swimmers than newly molted stage IV larvae and displayed considerable capacity to continue swimming at flow rates up to 9 $cm \cdot s^{-1}$. At each velocity there were observations of swimming over the 30-min period, and at 9 $cm \cdot s^{-1}$ the percentage of observations in which larvae were swimming ranged from 28 to 50 (Fig. 2F).

In addition to swimming, stage IV larvae maintained considerable mobility by crawling along the bottom and screens of the observation chamber. This crawling movement involved substrate contact with the walking legs and the normal pleopod beating with which stage IV larvae swim. In over 80% of the observations, control larvae were either swimming or crawling

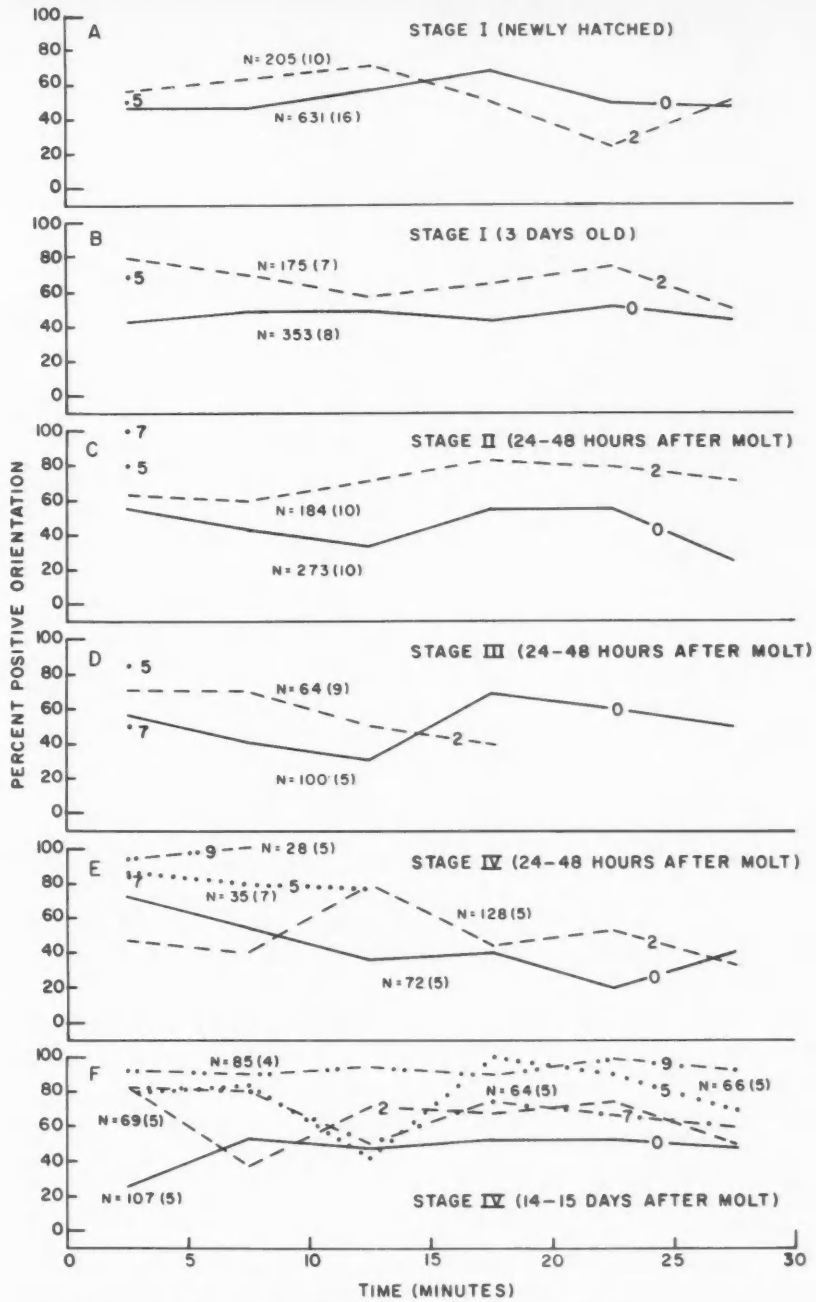


FIG. 3. Frequency of positive orientation in flowing water by larvae of *Homarus americanus*. Observations were at 30-s intervals and are summarized by 5-min periods for larvae that were swimming. Numbers in the lines are current velocities ($cm \cdot s^{-1}$); solid lines marked zero represent controls. $N$ = the number of observations, and in parentheses is the number of individual larvae observed.

(Table 1). Mobility of newly molted stage IV larvae was reduced to low levels (11% of the observations) at flow rates of 5 $cm \cdot s^{-1}$ and higher but older stage IV larvae remained quite mobile (64% of the observations) at these flow rates (Table 1).

In flowing water, the older stage IV larvae crawled (66% of the observations in which they were mobile) more than they swam but newly molted stage IV larvae swam a little more (59% of the observations at 2, 5, and 7 $cm \cdot s^{-1}$) than they crawled except at flow rates of 9 and 11.5 $cm \cdot s^{-1}$ where their limited mobility was more by crawling. The mobility of older

stage IV larvae at 11.5 $cm \cdot s^{-1}$ was accomplished entirely by crawling (Table 1).

### Orientation

For the controls, in 76–84% of observations on larvae that were swimming, orientation was either in the "upstream" or "downstream" direction over the 30-min period. This indicates that, in the absence of flow, orientation of the larvae was strongly influenced by the proximity of the sides of the observation chamber or by the fluorescent tubes directly above the surface. The frequency of positive orientation (i.e. "upstream" direction) by control larvae generally fluctuated around 50% over the 30-min observation period (Fig. 3).

In flowing water, the frequency of positive orientation by larvae that continued to swim was generally higher than for controls (Fig. 3). For stages I–III larvae, frequencies for controls for the 30-min period ranged from 45 to 52%, from 55 to 69% at a flow rate of 2 $cm \cdot s^{-1}$, and from 50 to 100% at higher flow rates (Table 2). For stage IV larvae, the frequency of positive orientation for controls was similar for each group at 47–48%. It was 49 and 67% at 2 $cm \cdot s^{-1}$ and ranged from 83 to 89% and from 70 to 94% at the higher flow rates for the newly molted and older stage IV larvae, respectively (Table 2).

## Discussion

Based on evidence indicating that all larval stages are restricted to a narrow depth range close to the surface, some authors (Dadswell 1979; Harding et al. 1983) argued that downstream transport of larvae by surface currents is a key mechanism of recruitment in the American lobster. Others (Squires 1970; Caddy 1979) argued that through behavioral responses to environmental stimuli they may move vertically to a great enough extent to maintain position near parental grounds by means of countercurrents. The latter hypothesis, or some modification of it, is an essential component of recruitment processes proposed for other decapod crustacean species (see Ennis 1983 for review) but papers describing these do not include consideration of a possible role for rheotactic responses of the larvae.

The observations reported here demonstrate that the rheotactic response is present in all larval stages of the American lobster. In stages I–III the response is weak in terms of the capability of larvae to swim against the current. A marked improvement in swimming ability occurs with the molt to stage IV which indicates that these larvae may be capable of directed swimming.

Conditions in the observation portion of the flow tank used in this study may not closely simulate the normal larval environment. Obvious differences are the turbulence associated with maintaining a flow of water in a tank and the proximity of visual reference points for the larvae. Hadley's (1906) experiments demonstrated that the rheotactic response in stage IV larvae could be elicited by an optical stimulus, i.e. a cardboard cylinder with slits that rotated around a motionless glass dish containing the larvae. It is conceivable that in the wild, where larvae are contained within a large mass of moving water, the rheotactic response is not present unless there is a visual or possibly some other cue which enables the larvae to "detect" the current. The phototactic response will override rheotaxis in stage IV larvae if light is introduced at an angle to the direction of current flow (Hadley 1906). In the wild, it may be that orientation of lobster larvae with respect to current direction and effort with respect to swimming against current flow is either reinforced or negated by the direction of incident light. Visual acuity of lobster larvae may be sufficient to enable them to detect current flow by visual reference to the sun, polarized light, clouds, stars, or the moon. Larvae of some decapod crustaceans are sensitive to polarized light (Via and Forward 1975; Bardolph and Stavn 1978), and Umminger (1968) showed that orientation to polarized light is involved in vertical migratory behavior of the copepod *Cyclops vernalis*. Close to shore, visual reference to the land mass or the sky–land interface may enable lobster larvae to detect current flow.

At any location in the sea, current speed and direction are variable because of interactions between wind speed and direction, tidal cycles, and general oceanic circulation. Intensity and direction of incident light also are variable. Considering the variability associated with light and current acting together, to which larvae are exposed continuously, a particular role for the rheotactic response as a larval recruitment mechanism is not obvious. Possibly, rheotaxis plays a role only in stage IV larvae where the response is particularly well developed.

The puerulus larva of spiny lobsters is comparable with the stage IV larva of the American lobster in that it also is the stage at which settlement occurs. The earlier (phyllosoma) larval stages are dispersed offshore and return of puerulus larvae to coastal areas where they settle apparently involves directed swimming over considerable distances (Serfling and Ford 1975; Phillips et al. 1978). Detection of underwater sound or wave surge may provide orientation for this directed swimming (Phillips and McWilliam 1986) but it is not known if rheotaxis is involved in the return of puerulus larvae to coastal areas. Directed swimming by stage IV larvae may also play a role in recruitment processes in the American lobster.

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## References

BARDOLPH, M., AND R. H. STAVN. 1978. Polarized light sensitivity in the stage I zoea of the mud crab, *Panopeus herbstii*. Mar. Biol. 46: 327–333.

CADDY, J. F. 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 204–216.

DADSWELL, M. J. 1979. A review of the decline in lobster (*Homarus americanus*) landings in Chedabucto Bay between 1956 and 1977 with an hypothesis for a possible effect by the Canso Causeway on the recruitment mechanisms of eastern Nova Scotia lobster stocks. Fish. Mar. Serv. Tech. Rep. 834: 114–144.

ENNIS, G. P. 1983. The effect of wind direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland nearshore area. Can. Tech. Rep. Fish. Aquat. Sci. 1138: 19 p.

HADLEY, P. B. 1906. The relation of optical stimuli to rheotaxis in the American lobster *Homarus americanus*. Am. J. Physiol. 17: 326–343.

HARDING, G. C., K. F. DRINKWATER, AND W. P. VASS. 1983. Factors influencing the size of the American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis. Can. J. Fish. Aquat. Sci. 40: 168–184.

MOLLER, T. H. 1978. Feeding behaviour of larvae and postlarvae of *Macro-*

*brachium rosenbergii* (de Man) (Crustacea: Palaeomonidae). J. Exp. Mar. Biol. Ecol. 35: 251–258.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

PHILLIPS, B. F., AND P. S. MCWILLIAM. 1986. The pelagic phase of spiny lobster development. Can. J. Fish. Aquat. Sci. 43: 2153–2163.

PHILLIPS, B. F., AND L. OLSEN. 1975. Swimming behaviour of the puerulus larvae of the western rock lobster. Aust. J. Mar. Freshwater Res 26: 415–417.

PHILLIPS, B. F., D. W. RIMMER, AND D. D. REID. 1978. Ecological investigations of the late-stage phyllosoma and puerulus larvae of the western rock lobster *Panulirus longipes cygnus*. Mar. Biol. 45: 347–357.

PHILLIPS, B. F., AND A. N. SASTRY. 1980. Larval ecology, p. 11–57. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 2. Academic Press, New York, NY. 390 p.

SERFLING, S. A., AND R. F. FORD. 1975. Ecological studies of the puerulus larval stage of the California spiny lobster, *Panulirus interruptus*. Fish. Bull. 73: 360–367.

SQUIRES, H. J. 1970. Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland 1960–65. Proc. Natl. Shellfish. Assoc. 60: 22–39.

SULKIN, S. D. 1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. Mar. Ecol. Prog. Ser. 15: 181–205.

VIA, S. E., AND R. B. FORWARD, JR. 1975. The ontogeny and spectral sensitivity of polarotaxis in larvae of the crab *Rhithropanopeus harrisi* (Gould). Biol. Bull. 149: 251–266.

VOGEL, S. 1981. Life in moving fluids: the physical biology of flow. Willard Grant Press, Boston, MA. 352 p.

UMMINGER, B. L. 1968. Polarotaxis in copepods. I. An endogenous rhythm in polarotaxis in *Cyclops vernalis* and its relation to vertical migration. Biol. Bull. 135: 239–251.

# Application of Laboratory Studies of Larval Behavior to Fisheries Problems

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Sulkin, S. D. 1986. Application of laboratory studies of larval behavior to fisheries problems. Can. J. Fish. Aquat. Sci. 43: 2184–2188.

An evaluation of the utility and constraints of an experimental approach to study of larval behavior is presented. Properly designed laboratory studies can provide a description of species-specific traits that contribute to vertical distribution and thus influence dispersal and recruitment. Results from such studies are most effectively applied to fisheries problems when field studies alone cannot provide sufficient information. Fisheries problems that require an understanding of the mechanistic basis of larval dispersal may also require the rigor and control provided by laboratory-based studies of larval behavior. A conceptual model of the physical and behavioral components determining vertical position of a plankter in the water column is presented as the basis for developing specific experiments that test for the direction and speed of passive and active movement. Data from these experiments permit development of hypotheses regarding larval dispersal and survival.

L'article présente une évaluation de l'utilité et des contraintes d'une méthode expérimentale destinée à l'étude du comportement des larves. Des expériences de laboratoire bien conçues peuvent fournir une description de traits spécifiques à une espèce qui contribuent à la répartition verticale et influencent ainsi la dispersion et le recrutement. Les résultats de telles études s'appliquent particulièrement bien aux problèmes de pêche lorsque les travaux sur le terrain ne suffisent pas à donner l'information nécessaire. Les problèmes de pêche qui demandent de comprendre l'aspect mécanique de la dispersion des larves peuvent aussi nécessiter la rigueur et les moyens de contrôle qu'offrent des études de laboratoire sur le comportement des larves. L'article présente un modèle conceptuel des composantes physiques et comportementales qui définissent la position verticale d'un planctonte dans la colonne d'eau; à partir de ce modèle, on peut construire des expériences précises permettant d'observer la direction et la vitesse de déplacement passif et actif. Les données obtenues grâce à ces expériences permettent d'élaborer des hypothèses concernant la dispersion et la survie des larves.

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Many marine and estuarine invertebrates, including commercially exploited decapods, have complex life cycles characterized by a planktonic larval stage of considerable duration. Upon release into the water column, larvae are subject to transport by prevailing circulation and, as a consequence, may be dispersed from the parental habitat. The settlement of some of these offspring in habitats favorable to post-metamorphic life is a principal factor in determining both population dynamics and distribution on a variety of scales.

Successful species have solved the problems associated with this type of life history. If we are to understand the underlying regulatory mechanisms of distribution and abundance of commercially exploited species to a level that permits predictive capability, we must learn the mechanistic basis — the process — of the entire dispersal phenomenon. This includes identification of transport mechanisms that determine whether or not offspring are retained within parental habitats and, for those that are not so retained, the subsequent mechanisms that ensure the recruitment of offspring to acceptable adult habitats.

Two general mechanisms of dispersion of invertebrate larvae have been proposed, namely stochastic processes or deterministic ones. In the former case, larval transport by ocean currents is not influenced by behavioral traits of the larvae. Larval distribution in the water column is random or caused strictly by eddy diffusion or other forms of hydrodynamic turbulence. It is important to note that these stochastic processes can produce predictable, directed horizontal transport under appropriate conditions. An example is provided by DeWolf (1974), who suggested that differential velocities of flooding and ebbing tidal currents in estuaries preferentially disperse barnacle cyprid larvae from the bottom up into the water column on flooding tides and thus effect net landward transport.

The deterministic alternative suggests that the complex array of behavioral responses exhibited by invertebrate larvae (see Sulkin 1984 for review of brachyuran larval behavior) influences distribution of larvae in the water column such that specific circulation patterns are exploited by the larvae to effect predictable, directional transport. Such "adaptive mechanisms" will be most effective when conservative hydrodynamic features are available for exploitation; that is, current patterns that are predictable on temporal and spatial scales. Because such circulation patterns tend to vary in the vertical plane in the estuarine and coastal marine environments and because many

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behavioral traits of larvae influence vertical movement, the vertical distribution of larvae is a key component of a deterministic mechanism. An example of this mechanism is provided by Bousfield (1955), again for barnacle larvae. Early larvae are concentrated in surface waters and are transported seaward in residual estuarine circulation, while later stages are deeper in the water column and are transported landward in a partially stratified estuary. These ontogenetic changes in vertical distribution effect retention of offspring within the parent estuary.

A third alternative combines aspects of stochastic and deterministic alternatives. Vertical distribution of larvae may be controlled by behavioral responses yielding predictable patterns, yet net directional transport may result only from episodic, rather than conservative, events. For example, Johnson (1982) has suggested that megalopae of the portunid crab *Callinectes sapidus* Rathbun are distributed primarily in the neuston in the water of the Middle Atlantic Bight continental shelf, but that onshore transport to the adult estuarine habitat results primarily from episodic wind events.

A key factor in evaluating the dispersal process of a particular species is the role played by larval behavior. A large and rapidly growing literature has described larval behavior using a variety of techniques (see recent papers by Mann and Wolf (1983) and Sulkin (1984) for review). The purpose of the present paper is to evaluate the use of laboratory experimental technique in the study of larval behavior. In the following sections, the utility and constraints of the experimental approach are discussed, a model for laboratory behavioral studies is reviewed, and a specific example of application of such research to a fisheries problem is presented.

## Advantages and Limitations of Experimental Behavioral Studies

A key component of dispersal is the pattern of vertical distribution that may result from behavioral regulation of depth. For a given species, how can such a phenomenon be documented? The obvious choices are to describe vertical distribution by means of a field sampling program or to define the array of behavioral traits exhibited by the species via laboratory experiments. The choice between these alternatives lies in the perception of the problem and the limitations imposed by each approach.

Traits that contribute directly to the dispersal process represent a deterministic component in the evolution of life histories; that is, heritable species-specific traits that relate to the successful recruitment of offspring to the adult phase and to conditions suitable for adult life. A variety of types of traits may be present: developmental mode, larval form, reproductive periodicity, and in the case of a dispersal phase, specific behavioral traits that influence vertical distribution and hence exploitation of estuarine and coastal circulation.

Field studies impose certain limitations in the examination of these specific traits. The vertical distribution of larvae in the field results from the net effects of a whole array of individual traits that may be interacting and also from localized hydrodynamic conditions that may be transient or atypical. Furthermore, changes in environmental conditions may influence component behavioral traits differently so that generalizations from limited sampling become tenuous. Ideally, distributions should be measured under the many different extant conditions that provide the necessary combinations of environmental stimuli. Such an approach often is logistically impossible and critical choices must be made in determination of such factors as sampling sites, gear type, and environmental conditions (weather, time of day, tide stage). Behavioral traits thus are inferred through a significant filter. Furthermore, in some cases, difficulties in identification of larvae blur the significance of the species as a systematic entity. Analysis of field samples may be possible only to the family or genus level (e.g. Christy and Stancyk 1982). Even congeneric species, however, may occupy different habitats and thus possess different traits related to recruitment to those habitats.

The point of laboratory investigation should be to avoid these problems, while producing rigorous data on behavioral traits. A consideration of limitations of the experimental approach thus becomes important.

The first point that should be obvious is that one should not attempt simply to transfer the water column to the laboratory. The small advantage gained in experimental control is lost in the reduction of realism. Furthermore, the experiments are still measuring net effects. An even worse alternative is to miniaturize the water column and assume that net change in distribution in response to stimulation is transferable to the real world. Under these circumstances, one has reduced realism, is still measuring net effects, and has introduced additional problems relating to scale effects. A metre-high observation chamber no more simulates the natural marine water column than a depression slide does a lake. Both, however, may prove to be useful tools in the laboratory investigation of specific questions.

For these reasons I propose a profoundly reductionist approach as most appropriate to experimental study of behavioral traits. The challenge is to design an experimental system that isolates the components that make up the behavioral repertoire of the species, measures them rigorously, and assigns to them their proper role in contributing to the dispersal process in nature.

## A Conceptual Model for Behavioral Studies

Sulkin (1984) described a conceptual model for the experimental study of behavioral regulation of depth in larvae. The model consists of three components.

The first component is the natural buoyancy of the larva. Assuming that the larva is a passive particle suspended in the water column, will it float upward (positive buoyancy) or sink downward (negative buoyancy)? This is the basis upon which activity on the part of the larva will act. The direction and rate of passive movement due to buoyancy can be measured readily by suspending narcotized larvae in a water column in the laboratory.

The second component of the model is orientation. The position of the larva in the water in response to directional cues is an active behaviorally regulated response (Fraenkel and Gunn 1961). In an animal such as a crab larva that swims via a power stroke, the orientation of the body will determine the direction of movement when swimming occurs (Foxon 1934; Sulkin 1973). Orientation therefore will determine whether locomotor activity on the part of the larva will complement the effects of buoyancy or compensate for it. The principal orienting stimuli that induce directional (taxis) response in the vertical plane are gravity and light (Fraenkel and Gunn 1961).

The third component of the model is level of locomotor activity. Speed and frequency of locomotion can be responsive to a number of environmental stimuli (Fraenkel and Gunn 1961). Of particular interest is the change in locomotor response that is induced by stimuli that vary in intensity with depth. This sort of response (kinesis) determines the degree to which the effects of buoyancy are modified by the larva's activity. Kinesis responses in crab larvae have been described for salinity, temperature, light, and hydrostatic pressure (see Sulkin 1984).

Vertical distribution results from dynamic balance among these various components such that, as one or more of the components changes, there may be predictable changes in vertical distribution based on species-specific traits.

Note that the specific questions that are presented by this model for experimental analysis are limited in scope: what is the sign of taxis response to light or to gravity; how does swimming activity change in response to specific kinds and degrees of stimulation? The experiments do not describe the vertical distributions of larvae; rather, they focus on the components of the phenomenon that can be addressed in a rigorous, quantitative fashion given the proper experimental design.

It may be further advantageous to employ a "base model" that is dependent upon the modifying effects on buoyancy of responses to the most conservative environmental parameters, those that are the most ubiquitous and predictable in the marine environment. Gravity as a taxis stimulus and hydrostatic pressure as a kinesis stimulus are examples. The base model can then be modified as appropriate by evaluating the modifying effects of behavioral responses to progressively less conservative (more variable) stimuli (e.g. light as a taxis stimulus; temperature as a kinesis stimulus).

This approach may be justified on both theoretical and logistical grounds. If there is selective advantage to the evolution of a combination of behavioral traits that regulate vertical movement of larvae, it is reasonable to suggest that selection has acted preferentially on responses to the most common and predictable stimuli. On logistical grounds, it is an approach that facilitates comparisons among species, by providing a common denominator for experimentation. For example, a comparison of base model responses between an estuarine and a marine species may show similarities (or differences) in fundamental traits that might be masked by behavioral sensitivity on the part of the estuarine species to the more highly variable stimuli typical of its habitat.

## Application of the Experimental Approach

Because an experimental approach to behavioral studies is necessarily limited in scope, it is most effectively applied to fisheries problems when field studies alone cannot provide sufficient unequivocal information and/or when the description of species-specific traits is essential. An example is provided by the study of larval recruitment in the portunid crab *Callinectes sapidus*. Patterns of larval dispersal and recruitment of young-of-the-year crabs to estuaries of the Middle Atlantic Bight have been the subject of many studies (Sulkin et al. 1980; Smyth 1980; Epifanio and Dittel 1982; Sulkin and Van Heukelem 1982; McConaugha et al. 1983; Provenzano et al. 1983; Epifanio et al. 1984; Sulkin and Epifanio 1986; Sulkin and Van Heukelem 1986). Although the species occupies estuaries during its juvenile and adult stages, its larvae require water of high salinity (Costlow et al. 1959). Larvae are released near the mouths of estuaries (Van Engel 1958) and frequently have been reported in waters of the continental shelf (Nichols and Keney 1963; Smyth 1980). Indeed, recent field studies indicate that larvae are exported from Chesapeake and Delaware bays immediately after hatching (Provenzano et al. 1983; Epifanio et al. 1984). The key question is whether blue crab larvae on the shelf are a source of future recruits or are lost from adult estuarine populations. Because of the high fecundity of the species (Van Engel 1958), a very small percent retention theoretically would be sufficient to account for successful larval recruitment. While the studies cited above present convincing circumstantial evidence that export of larvae is virtually complete and that recruitment of young-of-the-year individuals comes from offshore, the proof from the field is dependent upon negative evidence (e.g. the absence of later zoeal stages within the estuary).

This is a situation in which a description of species-specific traits that contribute to the dispersal mechanism becomes important. The following question can be asked: do first-stage blue crab larvae show adaptations that can promote retention in the face of obvious potential for export? Traits that regulate vertical distribution of the first zoeal instar are critical. It has been shown for a wide array of taxa, including crabs, that behavioral responses of early stages promote movement to the surface (Sulkin 1984). In partially stratified estuaries in which residual circulation is seaward at the surface and landward near the bottom, typical movement to the surface would position newly hatched *C. sapidus* larvae in seaward-flowing circulation (Pritchard 1952; Provenzano et al. 1983; Epifanio et al. 1984).

If the blue crab life history has evolved so as to promote retention within parental estuaries, one might predict adaptations in the hatching stage that result in avoidance of surface water. Do blue crab larvae show such traits or do they exhibit the more typical larval adaptations that promote movement to the surface?

Sulkin et al. (1980) described behavioral responses of first-stage *C. sapidus* larvae. The results can be evaluated within the context of the depth regulatory model described above. The first zoeal stage is negatively buoyant and sinks at a rate of 0.34 cm/s when narcotized.

However, responses to both gravity and light will position larvae so that swimming will result in upward movement. Geotaxis was defined by Fraenkel and Gunn (1961) as oriented movement in the vertical plane in the absence of light (downward: positive; upward: negative). Experimental methods used to document orientation often measure shifts in distribution of a sample of larvae over time. Orientation is thus inferred and it becomes essential to manipulate the experimental system so that results are unequivocal and, preferably, quantitative. Geotaxis poses a particularly difficult challenge, since changes in distribution in the vertical plane are confounded by buoyancy effects.

Sulkin et al. (1980) solved this problem by setting up two observation chambers, one oriented horizontally (control) and the other oriented vertically (experimental). Groups of sibling larvae were placed simultaneously at one end of the horizontal chamber and at the bottom end of the vertical chamber. Shifts in distribution in darkness were then compared between the two chambers. In theory, movement along the axis of the horizontal chamber should be due to nonoriented response (random swimming activity). Movement along the axis of the vertical chamber should be due to a combination of random movement, plus

any response that is oriented in the vertical plane.

Such experiments were run on replicate groups of stage I blue crab larvae that had been acclimated in three salinities (25, 30, 35 ppt). After 30 min, only a small fraction of each sample had moved from the end of the horizontal chamber in which the larvae had been placed. In contrast, about 90% of the sample had moved from the bottom to the top of the vertically oriented chamber. Clearly, movement in the vertical chamber exceeded that attributable to randomly directed swimming. It was concluded that the larvae exhibited negative geotaxis. Virtually all larvae in each replicate reacted in a similar fashion. Results in all three salinities were the same. Stage I blue crab larvae thus orient to the most predictable orienting stimulus such that swimming will result in upward movement.

Sulkin et al. (1983) reported that first-stage *C. sapidus* larvae respond positively to light in a wide range of intensities and wavelengths. However, because light is a highly variable and unpredictable stimulus in the marine environment (Sulkin 1984) and based on recent reports by Forward and Cronin (1979) and Forward et al. (1984) , it seems likely that taxis response to light may not be important in regulating vertical movement of crab larvae. To the extent that it stimulates orientation, however, it generally will complement the effects of geotaxis.

Locomotor activity is responsive to several stimuli that vary in intensity with depth in the estuarine and coastal marine environments. Salinity generally increases and temperature decreases with depth (Beardsley and Boicourt 1980), while hydrostatic pressure always increases with depth in a predictable manner. In keeping with the concept of the base model described earlier, response of larvae to increase in hydrostatic pressure was examined (Sulkin et al. 1980).

Stage I larvae showed an increase in swimming speed with pressure increments exceeding one additional atmosphere for larvae acclimated to 25, 30, or 35 ppt salinity. The response is the same shown for larvae of many other crab species, although the threshold for minimum response seems higher than is frequently the case (see Sulkin 1984).

Although there were no significant differences in swimming speed for larvae acclimated to the salinities in which they were tested, when larvae were tested in salinities higher than that of acclimation, their swimming speed increased (Sulkin et al. 1980). Surprisingly, however, swimming speed remained remarkably constant in the face of substantial temperature decease (Sulkin et al. 1980).

Behavioral traits thus orient stage I *C. sapidus* larvae such that swimming results in upward movement and conditions of salinity and pressure typical of increasing depth stimulate increased swimming activity. The first zoeal stage possesses behavioral traits that should promote movement toward the surface. Furthermore, the first larval stage can readily swim up through very sharp gradients in salinity (Sulkin and Van Heukelem 1982) and temperature (McConnaughey and Sulkin 1984). There are no species-specific heritable behavioral traits that should result in avoidance of surface water and hence promote estuarine retention. Indeed, when combined with other life history traits such as the requirement for high salinity during zoeal development (Costlow et al. 1959) and circumstantial evidence that hatching in *C. sapidus* is synchronized with ebbing tides (Provenzano et al. 1983; Epifanio et al. 1984), the behavioral repertoire of stage I *C. sapidus* larvae provides solid evidence that larval export is neither incidental nor serendipitous, but rather a fundamental life history characteristic.

The key to effective application of laboratory-based research lies in defining the questions properly, in designing the experiments in a way that exploits the control and rigor possible in the laboratory, and in recognizing the limitations and constraints of both laboratory and field approaches. Fisheries problems that require an understanding of the mechanistic basis of larval distribution are not only amenable to this experimental approach, but actually may require the rigor and control provided by laboratory-based behavioral studies.

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## References

BEARDSLEY, R. C., AND W. C. BOICOURT. 1980. On estuarine and continental shelf circulation in the Middle Atlantic Bight, p. 198–233. *In* B. A. Warren and C. Wunsch [ed.] Evolution of physical oceanography. MIT Press, Cambridge, MA.

BOUSFIELD, E. L. 1955. Ecological control of the occurrence of barnacles in the Miramichi estuary. Nat. Mus. Can. Bull. No. 137: 69.

CHRISTY, J. H., AND S. E. STANCYK. 1982. Timing of larval production and flux of invertebrate larvae in a well-mixed estuary, p. 489–503. *In* V. Kennedy [ed.] Estuarine comparisons. Academic Press, New York, NY.

COSTLOW, J. D. JR., G. H. REES, AND C. G. BOOKHOUT. 1959. Preliminary note on the complete larval development of *Callinectes sapidus* Rathbun under laboratory conditions. Limnol. Oceanogr. 4: 222–223.

DEWOLF, P. 1974. On the retention of marine larvae in estuaries. Thalassia Jugosl. 10: 415–424.

EPIFANIO, C. E., AND A. I. DITTEL. 1982. Comparison of dispersal of crab larvae in Delaware Bay, USA, and the Gulf of Nicoya, Central America, p. 477–487. *In* V. Kennedy [ed.] Estuarine comparisons. Academic Press, New York, NY.

EPIFANIO, C. E., C. C. VALENTI, AND E. E. PEMBROKE. 1984. Dispersal and recruitment of blue crab larvae in Delaware Bay, USA. Estuarine Coastal Shelf Sci. 18: 1–12.

FORWARD, R. B. JR., AND T. W. CRONIN. 1979. Spectral sensitivity of larvae from intertidal crustaceans. J. Comp. Physiol. 133:311–315.

FORWARD, R. B. JR., T. W. CRONIN, AND D. E. STEARNS. 1984. Control of diel vertical migration: photoresponses of a larval crustacean. Limnol. Oceanogr. 29: 146–154.

FOXON, G. E. H. 1934. Notes on the swimming methods and habits of certain crustacean larvae. J. Mar. Biol. Assoc. U.K. 19: 829–840.

FRAENKEL, G. S., AND D. L. GUNN. 1961. The orientation of animals. Dover Publications, New York, NY. 376 p.

JOHNSON, D. F. 1982. A comparison of recruitment strategies among brachyuran crustacean megalopae of the York River, lower Chesapeake Bay, and adjacent shelf waters. Ph.D. thesis, Old Dominion University, Norfolk, VA. 84 p.

MANN, R., AND C. C. WOLF. 1983. Swimming behavior of larvae of the ocean quahog, *Artica islandica* in response to pressure and temperature. Mar. Ecol. Prog. Ser. 13: 211–218.

MCCONAUGHA, J. R., D. F. JOHNSON, A. J. PROVENZANO, AND R. C. MARIS. 1983. Seasonal distribution of larvae of *Callinectes sapidus* (Crustacea: Decapoda) in the waters adjacent to Chesapeake Bay. J. Crustacean Biol. 3: 582–591.

MCCONNAUGHEY, R. A., AND S. D. SULKIN. 1984. Measuring the effects of thermoclines on the vertical migration of larvae of *Callinectes sapidus* (Brachyura: Portunidae) in the laboratory. Mar. Biol. 81: 139–145.

NICHOLS, P., AND P. M. KENEY. 1963. Crab Larvae (*Callinectes*) in plankton collections from cruises of M/V Theodore N. Gill, South Atlantic Coast of the United States, 1953–1954. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 448: 1–4.

PRITCHARD, D. W. 1952. Salinity distribution and circulation in Chesapeake Bay estuarine system. J. Mar. Res. 11: 106–123.

PROVENZANO, A. J., J. R. MCCONAUGHA, K. B. PHILLIPS, D. F. JOHNSON, AND J. CLARK. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. Estuarine Coastal Shelf Sci. 16: 489–499.

SMYTH, P. O. 1980. *Callinectes* (Decapoda Portunidae) larvae in the middle-Atlantic Bight, 1975–1977. Fish. Bull. U.S. 78: 251–265.

SULKIN, S. D. 1973. Depth regulation of crab larvae in the absence of light. J. Exp. Mar. Biol. Ecol. 13: 73–82.

1984. Behavioral basis of depth regulation in the larvae of brachyuran crabs. Mar. Ecol. Prog. Ser. 15: 181–205.

SULKIN, S. D., AND C. E. EPIFANIO. 1986. A conceptual model for recruitment of the blue crab, *Callinectes sapidus* Rathbun, to estuaries of the Middle Atlantic Bight, p. 117–123. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Pub. Fish. Aquat. Sci. 92.

SULKIN, S. D., AND W. VAN HEUKELEM. 1982. Larval recruitment in the crab *Callinectes sapidus* Rathbun: an amendment to the concept of larval retention in estuaries, p. 459–475. *In* V. Kennedy [ed.] Estuarine comparisons. Academic Press, New York, NY.

1986. Variability in megalopa duration and its consequence to dispersal in the portunid crab, *Callinectes sapidus* Rathbun. Bull. Mar. Sci. (In press)

SULKIN, S. D., W. VAN HEUKELEM, AND P. KELLY. 1983. Near-shore larval assemblages as a source of recruitment for estuarine and deeper sea invertebrates, p. 95–109. *In* J. B. Pearce [ed.] Reviews of water quality and transport of materials in coastal and estuarine waters. Cooperative Research Report No. 118, International Council for Exploration of the Sea, Copenhagen, Denmark.

SULKIN, S. D., W. VAN HEUKELEM, P. KELLY, AND L. VAN HEUKELEM, 1980. The behavioral basis of larval recruitment in the crab *Callinectes sapidus* Rathbun: a laboratory investigation of ontogenetic changes in geotaxis and barokinesis. Biol. Bull. 159: 412–417.

VAN ENGEL, W. 1958. The blue crab and its fishery in Chesapeake Bay. Part I. Reproduction, early development, growth, and migration. Commerc. Fish. Rev. 20: 6–17.

# Session 4
# Behavior and Movement

Chairman: W. F. Herrnkind

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# Relative Egg Production and Abundance of Berried Lobsters, *Homarus americanus*, in the Bay of Fundy and off Southwestern Nova Scotia

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Campbell, A., and D. S. Pezzack. 1986. Relative egg production and abundance of berried lobsters, *Homarus americanus*, in the Bay of Fundy and off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 2190–2196.

The relative abundance of berried female lobsters, *Homarus americanus*, and their contribution to total egg production in various areas of the Bay of Fundy and off southwestern Nova Scotia are estimated from sampling commercial and research cruise catches from traps. Concentrations of berried females occurred on Browns Bank, Georges Bank, and the New Brunswick side of the Bay of Fundy. To a lesser extent, berried females occurred in the coastal areas of southwestern Nova Scotia. Using a range of mortality values, a variety of population sizes were estimated from 1983 landings from which relative egg production values were calculated for each area. Lobsters from coastal waters of southwestern Nova Scotia combined with the Bay of Fundy were estimated to produce between 23 and 53% and those from the offshore Brown and eastern Georges Banks to produce between 47 and 77% of the region's total egg production. The results suggest that lobsters in each area are capable of producing large numbers of eggs. Where the resulting planktonic larvae settle as benthic juveniles is unclear.

Nous avons estimé l'abondance relative des femelles grainées de homard *Homarus americanus* et leur contribution à la production totale d'oeufs dans diverses régions de la baie de Fundy et du sud-ouest de la Nouvelle-Écosse en prélevant des échantillons des prises faites au casier, à la pêche commerciale et pendant des campagnes de recherche. Des concentrations de femelles grainées se trouvaient sur le banc Browns, sur le banc Georges et du côté néo-brunswickois de la baie de Fundy. Dans une moindre mesure, on en trouvait aussi dans les zones côtières du sud-ouest de la Nouvelle-Écosse. À partir d'une plage de valeurs de la mortalité, nous avons estimé un série de tailles des populations à partir des débarquements de 1983, et nous avons calculé la production relative d'oeufs pour chaque région. Les homards des eaux côtières du sud-ouest de la Nouvelle-Écosse et ceux de la baie de Fundy semblent produire entre 23 et 53 % du total de la production d'oeufs de la région, et ceux du large du banc Browns et de l'est du banc Georges semblent en produire entre 47 et 77 %. Ces résultats montrent que les homards de chaque région sont en mesure de produire une grande quantité d'oeufs. On ne sait toutefois pas où les larves planctoniques vont ensuite entamer leur phase benthique de juvéniles.

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Knowledge of the distribution of reproductive female lobsters, *Homarus americanus*, is important for understanding the source of larvae that recruit to a lobster stock. Previous studies of lobster size frequencies from samples of commercial lobster catches found few large mature lobsters in the traditional coastal fisheries of the Bay of Fundy and southwestern Nova Scotia areas (Fig. 1) but many large mature lobsters were found on the recently exploited outer shelf regions of Browns Bank and Georges Bank (Wilder 1974; Stasko and Campbell 1980; Stasko and Pye 1980). These results suggested that the main source of larvae for coastal southwestern Nova Scotia was from the large females on Browns Bank (Stasko 1978) and on Georges Bank (Harding et al. 1983). Those studies did not provide estimates of the relative abundance of mature lobsters and their egg contribution. The present paper provides information on the relative abundance of mature and berried (ovigerous) lobsters from recent sampling and estimates the relative egg contribution by lobsters from various areas in the Bay of Fundy and off southwestern Nova Scotia.

## Materials and Methods

Size frequencies, sex ratios, and proportion of berried females in trap catches were obtained by sampling lobsters at sea during commercial fishery activities in the following areas (Fig. 1): Lobster District 1 (LD1) including Dipper Harbour

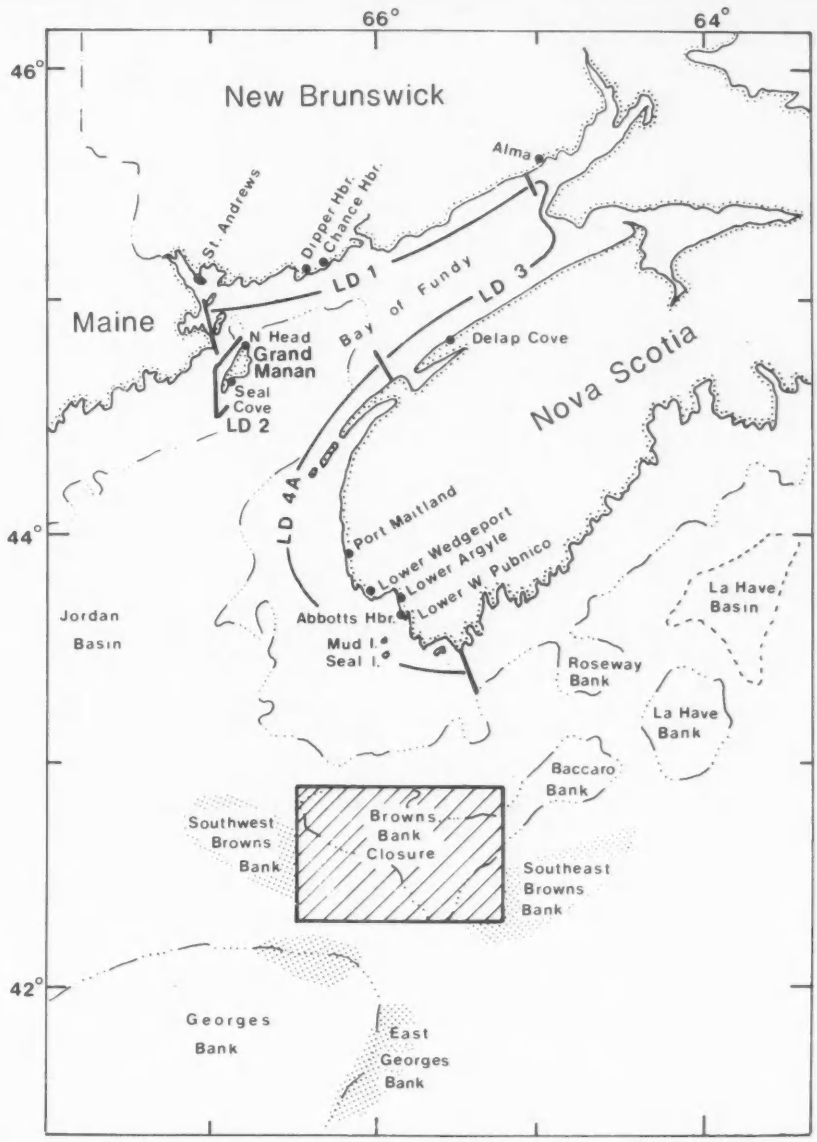


FIG. 1. Sampling areas in the Bay of Fundy and off southwestern Nova Scotia. Lobster districts (LD) are shown as lines in the coastal areas. Offshore area consists mainly of Browns Bank and Georges Bank beyond 93 km (50 naut. mi.) from the shoreline.

and St. Andrews and LD2 including Seal Cove and North Head during November 1983 – June 1984 (samples for North Head, November 1982 – June 1983, were included to increase sample size); LD3 including Alma and Delap Cove during October 1983 – July 1984; LD4A including Port Maitland, Lower Wedgeport, Lower West Pubnico, and Abbotts Harbour during December 1983 and May 1984; and offshore LDA including southeastern and southwestern Browns Bank during July 1983 and eastern Georges Bank (near Corsair Canyon) during June 1980 (Fig. 1). Additional samples from some of these areas and the closed Browns Bank area were obtained through research trapping surveys during closed fishing seasons of 1978–84 to compare the catch rates of berried females with new and old eggs (Table 1). The open fishing seasons were fall–spring for LD1 = second Wednesday in November to 14 January – 1 April to 29 June; LD2 = second Wednesday of November to fourth Thursday of June; LD3 = 15 October to 31 December – 1 March to 31 July; LD4A = last Tuesday in November to 31 May; LDA = open all year round. Data were also obtained from port samples (excluding ovigerous and prerecruit lobsters) for American commercial catches in Maine (J. Krouse, Maine Department of Marine Resources, W.

TABLE 1. Number of berried females per thousand trap hauls with only new or old eggs adjusted to 10°C. Samples selected from various locations in the Bay of Fundy and southwestern Nova Scotia. $N$ = number of berried females.

| Lobster district (LD) | Area | Date | No. per 1000 trap hauls at 10°C | Egg state | Percent with old eggs | Percent of total females | $N$ | No. of trap hauls | Temperature (°C) |
|---|---|---|---|---|---|---|---|---|---|
| LD 1 | Chance Harbour | 1–15 Aug. 1980 | 56 | Old | 93.8 | 8.5 | 17 | 280 | 10.2 |
| LD 2 | Seal Cove | 16–31 July 1978 | 100 | Old | 97.0 | 9.6 | 35 | 341 | 10.0 |
| | North Head | 16–30 Oct. 1982 | 346 | New | 0 | 46.8 | 370 | 973 | 11.0 |
| | | 16–31 July 1983 | 243 | Old | 99.4 | 37.2 | 164 | 672 | 10.0 |
| LD 3 | Alma | 1–15 Sept. 1979 | 361 | New | 2.7 | 45.8 | 223 | 417 | 14.4 |
| | | 16–31 July 1980 | 105 | Old | 94.3 | 36.2 | 158 | 1134 | 12.5 |
| | | 1–15 July 1983 | 117 | Old | 97.2 | 22.2 | 36 | 259 | 11.5 |
| | Delap Cove | 1–15 July 1982 | 57 | Old | 100.0 | 15.6 | 5 | 97 | 9.0 |
| LD 4A | Inshore areas | | | | | | | | |
| | Lower West Pubnico | 17–28 Sept. 1984 | 210 | New | 3.3 | 6.9 | 30 | 92 | 15.0 |
| | Mud Island (west) | 17–28 Sept. 1984 | 146 | New | 0 | 9.4 | 5 | 28 | 12.2 |
| | Seal Island | 1–15 Aug. 1979 | 103 | New | 38.6 | 5.3 | 44 | 248 | 10.6 |
| | Lower Wedgeport | 16–31 July 1983 | 21 | Old | 100.0 | 4.3 | 6 | 281 | 10.0 |
| | Lower Argyle | 15–31 July 1983 | 12 | Old | 100.0 | 0.7 | 7 | 442 | 13.7 |
| | Offshore areas | | | | | | | | |
| | SE Browns Bank | 19–24 July 1983 | 80 | Old | 89.0 | 9.1 | 137 | 1682 | 9.0 |
| | SW Browns Bank | 18–21 July 1983 | 65 | Old | 89.0 | 5.0 | 55 | 841 | 9.0 |
| | Browns Bank closure | 25 Sept. – 2 Oct. 1980 | 479 | New | 0 | 79.2 | 100 | 174 | 12.0 |
| | | July 1985 | 260 | Old | 98.2 | 22.1 | 451 | 1700 | 10.0 |
| | Georges Bank | 14–22 June 1980 | 340 | Old | 100.0 | 15.8 | 347 | 1022 | 10.0[a] |

[a]Temperature unknown.

Boothbay Harbor, ME, pers. comm.) and eastern Georges Bank (M. J. Fogarty, National Marine Fisheries Service, Woods Hole, MA, pers. comm.) during 1983.

Records of Canadian and American lobster landings (tonnes) for 1983–84 were obtained from Statistics Canada, Halifax, and J. Krouse and M. J. Fogarty, respectively. Bottom water temperatures were obtained with reversible thermometers, bathythermographs, and continuous recording thermographs set on lobster grounds.

Eggs of berried females were examined and classified as "old" with developed embryos or about to hatch and as "new," recently extruded eggs with no embryo or eye pigmentation. Female lobsters carry their eggs for 9–12 mo. Egg extrusion and hatch usually occur during July–October in the areas studied.

As an example, selected locations were chosen to show the relative abundance of berried females with only new or old eggs. To correct for the effect of temperature on lobster catchability (McLeese and Wilder 1958), a simple standardization of the catch per trap haul data with temperature was used. The number of berried females per thousand trap hauls ($F$) was arbitrarily standardized to 10°C according to the equation

$$(1)\quad F = \frac{B \cdot G \cdot 10 \cdot 1000}{H \cdot T}$$

where $B$ = the number of berried females caught per area, $G$ = proportion of total berried females with old or with new eggs in relation to total berried females, $H$ = number of trap hauls, and $T$ = local bottom temperature (degrees Celsius). Unfortunately, there are no data to standardize lobster catchability with temperature that are of general applicability to all the areas examined. The standardization in this study assumes a 1:1 relationship between temperature and catchability which probably is not precisely correct, as McLeese and Wilder (1958) indicated a proportionality constant that differs from 1. However, we could not use the data from McLeese and Wilder (1958) because the catchability indices obtained were dependent on local stock densities having no direct applicability to other areas.

Sex ratios were calculated by dividing the number of males, females (both berried and nonberried females), or berried females by the total number of lobsters in each 5-mm carapace length (CL) group. Lobsters were considered immature (<95 mm CL) and mature (≧95 mm CL) based on the median size at physiological maturity (Campbell 1983; A. Campbell, unpubl. data) estimated by the ovary examination technique (Aiken and Waddy 1980).

Size frequencies were weighted, according to seasonal (3-mo periods) landings within each lobster district, and then combined for all areas (LD1–LD4A and offshore LDA) according to the 1983 landings for each area into an overall size frequency of recruits (legal-sized lobsters) for 1983. Although the most appropriate weighting factor is population size, this value was not available for each area. Exploitation rates are high enough in most areas to remove 60–95% of recruited lobsters each year (Anthony 1980; Campbell 1980; Fogarty et al. 1982). Thus, exploitation rates are assumed to be sufficiently high in most years so that landings are a reasonable proxy for approximate population size.

The relative total egg production ($E_i$) for each area was estimated with the equations 2, 3, and 4:

$$(2)\quad E_i = S \cdot N_i \cdot P_i \cdot Q_i$$

where $E_i$ = total number of eggs in size class $i$ (millimetres CL), $N_i$ = fraction of the total recruits in size class $i$, $P_i$ = fraction of berried females of total males and females in size class $i$, $Q_i$ = average number of eggs per female in size class $i$, and $S$ = recruited stock size in numbers which is calculated

TABLE 2. Estimated range of egg production, total annual mortality, landings, mean weight, and median carapace length of legal-sized lobsters from the Bay of Fundy and off southwestern Nova Scotia during 1983. Values in parentheses are percentages of total.

| Lobster district (LD) | Area | Estimated egg numbers ($\times 10^6$) Minimum[a] | Maximum[b] | Total annual mortality ($A$) Upper[a] | Lower[b] | Landings (t) | Lobster Mean weight (kg) | Lobster Median CL (mm) |
|---|---|---|---|---|---|---|---|---|
| LD 1 | Dipper Harbour and St. Andrews | 171 (3.0) | 363 (1.8) | 0.85 | 0.4 | 210 (3.3) | 0.631 | 88 |
| LD 2 | Seal Cove | 55 (1.0) | 118 (0.6) | 0.85 | 0.4 | 288 (4.5) | 0.566 | 88 |
| | North Head | 223 (4.0) | 1 117 (5.5) | 0.5 | 0.1 | 43 (0.7) | 1.954 | 119 |
| LD 3 | Alma and Delap Cove | 121 (2.1) | 283 (1.4) | 0.7 | 0.3 | 127 (2.0) | 0.788 | 94 |
| LD 4A | Inshore areas | 2405 (42.5) | 5 111 (25.0) | 0.85 | 0.4 | 5148 (79.8) | 0.580 | 88 |
| | Offshore areas | | | | | | | |
| | SE Browns Bank | 483 (8.5) | 2 415 (11.8) | 0.5 | 0.1 | 114 (1.7) | 1.620 | 122 |
| | SW Browns Bank | 549 (9.7) | 2 748 (13.5) | 0.5 | 0.1 | 200 (3.1) | 1.290 | 112 |
| | E Georges Bank | 1650 (29.2) | 8 253 (40.4) | 0.5 | 0.1 | 317.5[c] (4.9) | 1.850 | 125[d] |
| | Total | 5657 | 20 408 | | | 6447.5 | | |

[a]Based on upper values of $A$.
[b]Based on lower values of $A$.
[c]Includes Canadian (156 t) and American (161.5 t) landings.
[d]Includes Canadian (129 mm median CL) and American (116 mm median CL).

as

$$(3)\quad S = \frac{Y}{W \cdot A}$$

where $Y$ = annual yield (landings) (kilograms), $W$ = average weight (kilograms) per recruit, and $A$ = total annual mortality of lobsters as a proportion.

Values of $E_i$ are accumulated for each size class $i$, and the total egg production ($E_t$) for all size classes is

$$(4)\quad E_t = \sum_{i=1}^{\max} E_i$$

where max is the size of the largest size class of berried females. The formula for fecundity of berried lobsters with old eggs, $Q_i$ (from Campbell and Robinson 1983), is

$$Q_i = 0.00256X^{3.409}$$

where $X$ = carapace length (millimetres).

Berried females with old eggs were less frequent (this study) and carried fewer eggs (Perkins 1971) than newly berried females. Consequently, only size frequencies having berried females with eggs more than 4 mo old were used to calculate egg production. Overall weighted size frequency and egg production for the whole of the Gulf of Maine and for all offshore adjoining areas were not calculated because up-to-date information on berried female lobsters was not available from port samples for either the State of Maine or the southwest Georges Bank lobster fisheries.

The results of the present study must be considered in relative terms because bias may be introduced with trap data used to estimate brood stock abundance and distribution. Standardization of traps is difficult because catching efficiency can vary from area to area and between seasons due to different activity levels of lobsters related to temperature changes (McLeese and Wilder 1958), changes in density and dispersion of lobsters, physiological condition of the lobsters, and different selectivity of lobster sizes due to variation in entrance hole and escape vent dimensions (Krouse and Thomas 1975; Elner 1980).

## Results

### Size Frequencies

Lobsters at sizes of 65–95 mm CL were plentiful in fishermen's traps from shallow waters (<70 m) off southern Grand Manan and coastal areas of the Bay of Fundy (lower half) and off southwestern Nova Scotia where the recruit size is 81 mm CL (Fig. 2). These areas (e.g. LD1, southern LD2, and LD4A) provided 87.6% of the 1983 Canadian landings and were composed of lobsters that had a median CL of 88 mm (Table 2). Similarly, for coastal Maine, which had high 1983 lobster landings (9968 t), the median CL was 88 mm (J. Krouse, pers. comm.). In contrast, lobsters from North Head (Grand Manan), the upper reaches of the Bay of Fundy (Campbell 1984), and Browns Bank and Georges Bank areas accounted for 12.4% of the 1983 landings, had large lobsters, mostly >90 mm CL, and the median CL was >100 mm (Fig. 2; Table 2).

A total overall weighted size frequency of recruits for all areas indicated that 65.1% were in the first molt group beyond legal size (81–94 mm CL) and 34.9% were mostly mature (>94 mm CL) (Fig. 3).

### Sex Ratio

Sex ratio of immature lobsters (<95 mm CL) was approximately 1:1 (Fig. 4). For mature lobsters, there was a higher proportion of females in the smaller size groups (95–119 mm CL) and a higher proportion of males in the larger size groups (>120 or >140 mm CL), depending on the area (Fig. 4). These uneven sex ratios may be caused by a higher fishing mortality of males than females because berried females are protected (Skud 1969; Skud and Perkins 1969; Ennis 1980) and because of faster growth rates of males than females after sexual maturity (Campbell 1983).

### Berried Females

Usually there were 30–70% fewer berried females with old

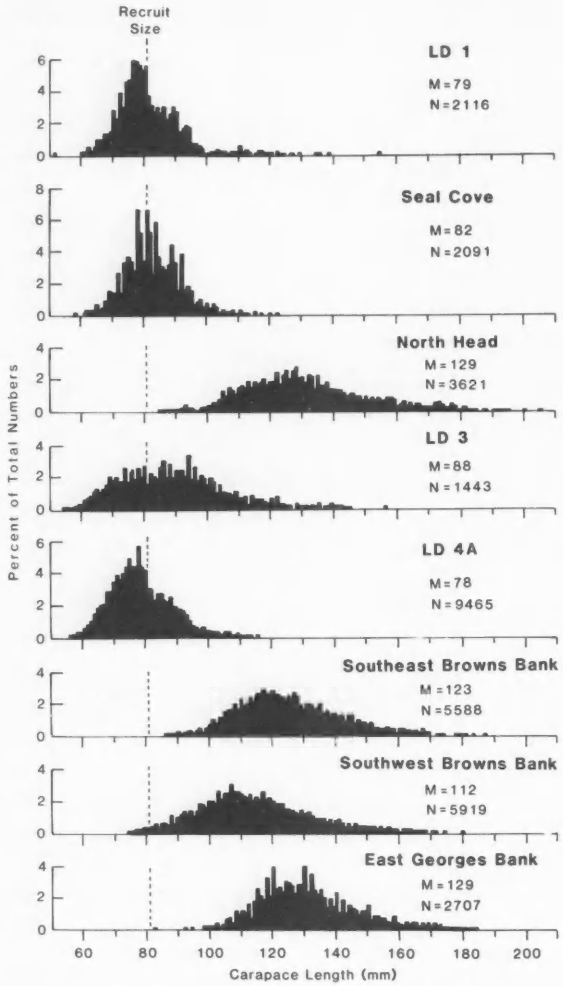


FIG. 2. Size frequencies (% in 1-mm CL groups of total sample) of lobsters caught in fishermen's traps in eight areas in the Bay of Fundy and off southwestern Nova Scotia. $M$ = median mm CL; $N$ = number of lobsters in sample.

eggs than with new eggs (Table 1). Overall, between 100 and 479 newly berried females were caught per 1000 trap hauls during August–October, making up 5.3–79.2% of legal-sized females caught (Table 1). Many berried females were caught in the Browns Bank closure area and on the New Brunswick side of the Bay of Fundy. Although the fewest berried females were caught in LD4A, as many as 210 berried females per 1000 trap hauls with new eggs were caught in the inshore areas of Lobster Bay (Lower West Pubnico) (Table 1). A similar geographic trend in relative abundance was observed during July–August for berried females with old eggs about to hatch.

The smallest and largest berried females measured in various at-sea commercial trap samples during 1983–84 were 89 and 191 mm CL from the Bay of Fundy, 82 and 125 mm CL in coastal southwestern Nova Scotia (140 mm CL for one off Seal Island during 1979), and 89 and 191 mm CL offshore on Browns Bank. Berried females as small as 84 mm CL and as

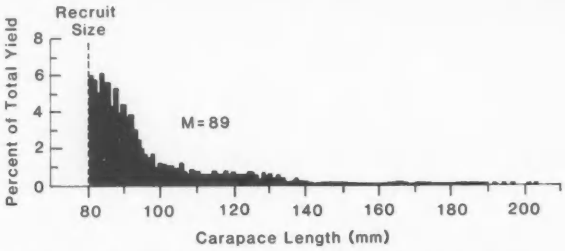


FIG. 3. Overall weighted size frequency of total catch (as yield) for recruited lobsters in the Bay of Fundy, off southwestern Nova Scotia, Browns Bank, and eastern Georges Bank (including American landings) during 1983. $M$ = median mm CL.

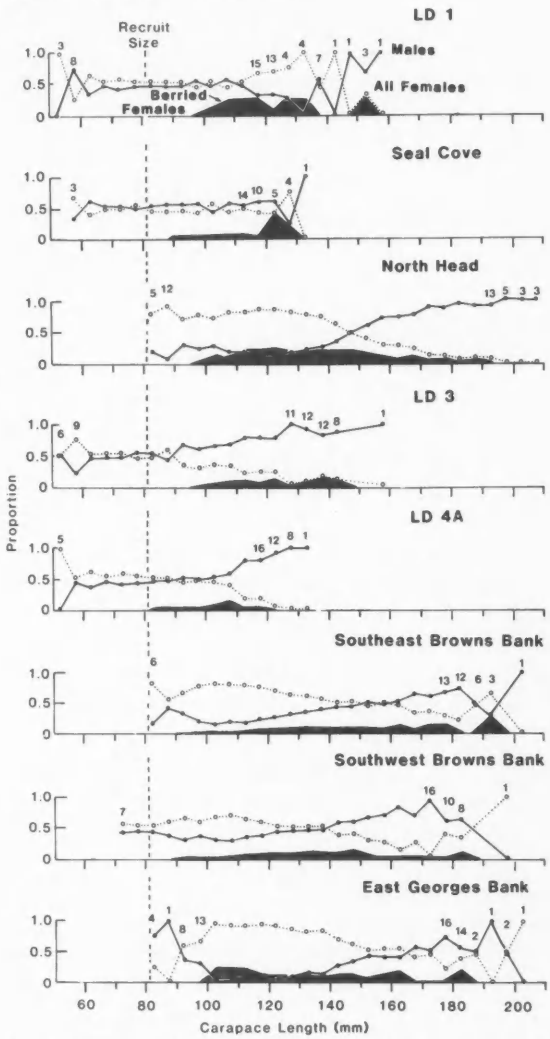


FIG. 4. Proportion of males, females, and berried females per total lobsters in 5-mm CL groups for eight areas in the Bay of Fundy and off southwestern Nova Scotia during 1983–84. Data from same samples as in Fig. 2. The number of lobsters in each 5-mm CL group usually was greater than 100; numbers less than 20 are shown above appropriate sex ratio.

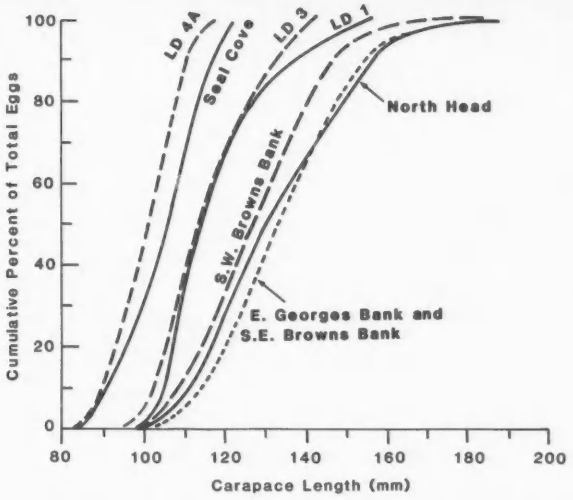


FIG. 5. Cumulative percent of total egg production by female lobsters at different sizes for each of eight areas of the Bay of Fundy and southwestern Nova Scotia during 1983–84.

large as 200 mm CL were recorded from Lyndonia Canyon, Georges Bank, during 1971 (D. G. Wilder and D. E. Graham, unpubl. data). Ovigerous females in commercial samples generally did not constitute more than a quarter of the total catch or more than half of the total female catch in any 5-mm CL group (Fig. 4).

### Egg Production

Egg production should be considered in relative terms. Calculation of egg production is based on the relative number of lobsters with old eggs in each size group, and the stock size is estimated from the local lobster landings and range of total annual mortality values ($A$) for recruits. The $A$ values for various areas were chosen arbitrarily to represent the minimum and maximum values calculated previously (Paloheimo 1963; Anthony 1980; Campbell 1980; Campbell and Duggan 1980; Fogarty et al. 1982).

The relative contribution to total number of eggs by various size classes (Fig. 5) is a reflection of the local size frequency of berried females. The onset of egg production varied for females from 82 to 100 mm CL, and for most inshore areas the median (or 50% of total egg production) was from lobsters between 100 and 115 mm CL whereas for the offshore areas (Browns Bank and Georges Bank) and North Head, the median was between 126 and 132 mm CL (Fig. 5). Most (>70%) egg production was from females of 100–143 mm CL (Fig. 5), which is similar to that predicted by an egg-per-recruit model (Campbell and Robinson 1983).

The percentage contribution to total egg production by lobsters in the coastal areas (including the Bay of Fundy) was 52.6% and for the offshore areas (Browns Bank and Georges Bank) was 47.4%, with $A$ values set at the high upper levels (Table 2). For low values of $A$, the inshore areas contributed 34.3% and the offshore areas 65.7% of total egg production (Table 2). Assuming the highest $A$ values for the inshore areas (including North Head with low $A$ value of 0.1) but the lowest $A$ values for the offshore areas, relative egg production would be 23.1 and 76.9%, respectively. Lobsters from eastern Georges Bank and LD4A contributed the most to egg production (Table 2).

## Discussion

The generally low proportion of berried females in the samples (Fig. 4) probably was due to a combination of factors such as egg extrusion occurring in alternate years (Aiken and Waddy 1980), lower trapability (Templeman and Tibbo 1945), sexual variation in exploitation rates (Ennis 1980), and seasonal movements of mature females between deep and shallow waters (Cooper and Uzmann 1971; Campbell and Stasko 1986). Also, the samples were taken when females with older eggs were less abundant in traps than those with new eggs (Table 1). The effect of total egg loss by some females would also cause the proportion of berried females captured in a sample to decrease. Tagging studies (Campbell 1986; Campbell and Brattey 1986) off North Head during 1982–83 indicated that the reduction in catch rate of berried females (Table 1) could be attributed partially to total egg loss. Campbell and Brattey (1986) found that, of the newly berried females tagged during July–October 1982, the percentage of recaptured females that had lost all their eggs increased from 1% in March to about 20% by mid-August 1983. Some tagged berried females had multiple (2–10) recaptures (Campbell 1986) suggesting that some lobsters are trapable throughout much of the egg development period. Egg loss from females can be attributed to repeated trapping and handling by fishermen, inadequate egg adhesion (Aiken and Waddy 1980), nemertean predation feeding on eggs (Waddy and Aiken 1985), fouling by microbial epibionts (Harper and Talbot 1984), cleaning or grooming of eggs by ovigerous lobsters (Aiken et al. 1985), and early hatching of larvae. Ideally, the brood stock size should be estimated during early summer (June–mid-July), just prior to hatching when many berried females are moving to or have moved to shallow waters of the coastal areas or the offshore banks. Unfortunately, this relatively short period occurs during the closed fishing season in most inshore areas. Also, the Browns Bank closure area is closed to commercial fishing. Despite problems of using data from trap sampling, our study provides a reasonable picture of the range in relative reproductive potential of lobsters from the areas studied. Many of the size frequencies from various areas have not changed significantly over the last 5–10 yr (Stasko and Campbell 1980; Stasko and Pye 1980; Pezzack and Duggan 1983, 1985; Campbell 1984), suggesting a relatively stable size structure.

Berried females with eggs about to hatch have been found concentrated on Browns Bank, Georges Bank, and the New Brunswick side of the Bay of Fundy during the summer months (Table 1). To a lesser extent, berried females were found in the coastal waters of southwestern Nova Scotia. Estimated relative egg production, from commercial and research catches, indicated that lobsters in the coastal waters of southwestern Nova Scotia and Bay of Fundy may have produced between 23 and 53% and those from offshore Browns Bank and eastern Georges Bank between 47 and 77% of total eggs during 1983. The results are different from previous studies which suggested that few eggs were produced in the coastal areas (Wilder 1965, 1974; Stasko 1978; Stasko and Campbell 1980). Indeed, our results suggest that most of these coastal and offshore areas are capable of producing many lobster eggs. How many eggs are required to produce sufficient numbers of larvae to maintain a

stable recruited lobster population is unknown. Also, where the free-swimming larvae eventually settle as benthic juveniles is unknown.

The source of larvae that recruit to coastal southwestern Nova Scotia may be a local phenomenon in some areas, not necessarily dependent on imported larvae, and/or may be based partially on long-distance larval drift from Browns Bank, Georges Bank, or the eastern shore of Nova Scotia (Stasko and Campbell 1980; Harding et al. 1983). Whether or not larval recruitment comes primarily from inside or outside the Bay of Fundy is uncertain. Residual surface currents tend to flow into the Bay of Fundy on the Nova Scotia side and out of the Bay on the New Brunswick side (Bumpus and Lauzier 1965). Larvae from females from the offshore banks or coastal areas of southwestern Nova Scotia may enter and settle in the Bay of Fundy. Larvae from females on the New Brunswick side of the Bay of Fundy may be swept by surface currents along the Gulf of Maine coastline, or may be caught in eddies within bays along the mainland coast or the southern coast of Grand Manan (Campbell 1985). In these locations, the fishery is usually productive, with most lobsters caught being subadult and close to the recruit size. Consequently, further studies on lobster larval ecology are required.

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## References

AIKEN, D. E., AND S. L. WADDY. 1980. Reproductive biology of lobsters, p. 215–276. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 1. Academic Press, New York, NY. 463 p.

AIKEN, D. E., S. L. WADDY, AND L. S. UHAZY. 1985. Aspects of the biology of *Pseudocarcinonemertes homari* and its association with the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 351–356.

ANTHONY, V. C. 1980. Review of lobster mortality estimates in the United States. Can. Tech. Rep. Fish. Aquat. Sci. 932: 17–26.

BUMPUS, I. F., AND L. M. LAUZIER. 1965. Surface circulation on the continental shelf of eastern North America between Newfoundland and Florida. Ser. Atlas of the Mar. Environ., Folio 7. American Geographical Society, New York, NY.

CAMPBELL, A. 1980. A review of mortality estimates of lobster populations in the Canadian Maritimes. Can. Tech. Rep. Fish. Aquat. Sci. 932: 27–35.

1983. Growth of tagged American lobsters, *Homarus americanus*, in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 40: 1667–1675.

1984. Aspects of lobster biology and fishery in the upper reaches of the Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1256: 469–489.

1985. Application of a yield and egg-per-recruit model to the lobster fishery in the Bay of Fundy. N. Am. J. Fish. Manage. 5: 91–104.

1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. Can. J. Fish. Aquat. Sci. 43: 2197–2205.

CAMPBELL, A., AND J. BRATTEY. 1986. Egg loss from the American lobster, *Homarus americanus*, in relation to nemertean *Pseudocarcinonemertes homari*, infestation. Can. J. Fish. Aquat. Sci. 43: 772–780.

CAMPBELL, A., AND D. R. DUGGAN. 1980. Review of the Grand Manan lobster fishery with an analysis of recent catch and effort trends. Can. Tech. Rep. Fish. Aquat. Sci. 997: 20 p.

CAMPBELL, A., AND D. G. ROBINSON. 1983. Reproductive potential of three lobster (*Homarus americanus*) stocks in the Canadian Maritimes. Can. J. Fish. Aquat. Sci. 40: 1958–1967.

CAMPBELL, A., AND A. B. STASKO. 1986. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. Mar. Biol. (In press)

COOPER, R. A., AND J. R. UZMANN. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science (Wash., DC) 171: 288–290.

ELNER, R. W. 1980. Lobster gear selectivity — a Canadian overview. Can. Tech. Rep. Fish. Aquat. Sci. 932: 77–83.

ENNIS, G. P. 1980. Size–maturity relationships and related observations in Newfoundland populations of the lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 37: 945–966.

FOGARTY, M. J., R. A. COOPER, J. R. UZMANN, AND T. BURNS. 1982. Assessment of the USA offshore American lobster (*Homarus americanus*) fishery. Int. Counc. Explor. Sea C.M. 1982/K:14: 21 p.

HARDING, G. C., K. F. DRINKWATER, AND W. P. VASS. 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis. Can. J. Fish. Aquat. Sci. 40: 168–184.

HARPER, R. E., AND P. TALBOT. 1984. Analysis of the epibiotic bacteria of lobster (*Homarus*) eggs and their influence on the loss of eggs from the pleopods. Aquaculture 36: 9–26.

KROUSE, J., AND J. C. THOMAS. 1975. Effects of trap selectivity and some population parameters on size composition of the American lobster, *Homarus americanus*, catch along the Maine coast. Fish. Bull. U.S. 73: 862–871.

MCLEESE, D. W., AND D. G. WILDER. 1958. The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. J. Fish. Res. Board Can. 15: 1345–1354.

PALOHEIMO, J. E. 1963. Estimation of catchabilities and population sizes of lobsters. J. Fish. Res. Board Can. 20: 59–88.

PERKINS, H. C. 1971. Egg loss during incubation from offshore northern lobsters (Decapoda:Homaridae). Fish. Bull. U.S. 69: 431–453.

PEZZACK, D. S., AND D. R. DUGGAN. 1983. The Canadian offshore lobster (*Homarus americanus*) fishery — 1971 to 1982. Int. Counc. Explor. Sea C.M. 1983/K:34: 15 p.

1985. The Canadian offshore lobster fishery 1971–1984: catch history, stock condition and management options. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 85/89: 26 p.

SKUD, B. E. 1969. The effect of fishing on size composition and sex ratio of offshore lobster stocks. Fiskeridir. Skr. Ser. Havunders. 15: 259–309.

SKUD, B. E., AND H. C. PERKINS. 1969. Size composition, sex ratio and size at maturity of offshore northern lobsters. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 598: 10 p.

STASKO, A. B. 1978. Inshore–offshore SW Nova Scotia lobster stock interaction: an hypothesis. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 78/37: 10 p.

STASKO, A. B., AND A. CAMPBELL. 1980. An overview of lobster life history and fishery in southwestern Nova Scotia. Can. Tech. Rep. Fish. Aquat. Sci. 954: 208–224.

STASKO, A. B., AND R. W. PYE. 1980. Geographical size differences in Canadian offshore lobsters. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 80/47: 11 p.

TEMPLEMAN, W., AND S. N. TIBBO. 1945. Lobster investigation in Newfoundland 1938 to 1941. Nfld. Dep. Nat. Resour. Res. Bull. (Fish.) 16: 98 p.

WADDY, S. L., AND D. E. AIKEN. 1985. Immunofluorescent localization of American lobster egg yolk protein in the alimentary tract of the nemertean *Pseudocarcinonemertes homari*. Can. J. Fish. Aquat. Sci. 42: 357–359.

WILDER, D. G. 1965. Lobster conservation in Canada. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 156: 21–29.

1974. Inshore and offshore lobster stocks. Fish. Res. Board Can. MS Rep. 1293: 14 p.

# Migratory Movements of Ovigerous Lobsters, *Homarus americanus*, Tagged off Grand Manan, Eastern Canada

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A total of 2139 ovigerous lobsters, *Homarus americanus*, were tagged and egg development recorded off Grand Manan, eastern Canada, during 1982–83. Recaptures during August 1982 to January 1984 totaled 1877, representing 1046 individuals including 457 that were captured 2–10 times. The single recapture data indicate that the majority (75%) of the lobsters moved <15 km. Use of distance moved information from single recaptures of lobsters at liberty for long periods can be misleading, since exact distance moved between tag release–recapture points usually is unknown. Multiple recapture and depth at recapture data gave more information on the movements of the lobsters. Many lobsters showed seasonal shallow-deep migrations of >20 km with recaptures in shallow (<20 m) water during summer–fall and in deep (>200 m) water during winter–spring. Many ovigerous females returned to the Grand Manan area the following summer. A few (7%) moved north >30 km into the Bay of Fundy and south as much as 322 km along the coastline of Maine. Examination of the multiple recapture data between months indicated positive correlations between change in depth, distance moved, and water temperature. The seasonal depth migrations of ovigerous lobsters appear to be associated with maximizing temperatures which provide sufficient degree-days for completion of egg development. Also, hatching eggs in relatively warm shallow waters may confer a survival advantage for pelagic lobster larvae by decreasing development time to the benthic stage.

En 1982–83, au large de Grand Manan, dans l'est du Canada, 2 139 homards (*Homarus americanus*) ovigères ont été marqués, et le développement des oeufs a été surveillé. Entre août 1982 et janvier 1984, 1 877 homards ont été recapturés, ce qui représente 1 046 spécimens dont 457 ont été repris de 2 à 10 fois. Les données sur les recaptures uniques indiquent que la majorité (75 %) des homards s'étaient déplacés de moins de 15 km. Il peut être trompeur d'utiliser la distance parcourue en cas de recapture unique par des homards laissés libres pendant de longues périodes car on ne connaît pas la distance exacte parcourue entre les points de libération après marquage et de recapture. Les recaptures multiples et la profondeur de recapture donnent davantage d'information sur le déplacement des homards. De nombreux homards effectuent des migrations saisonnières entre les zones profondes et peu profondes de plus de 20 km, les recaptures en eaux peu profondes (< 20 m) ayant lieu pendant l'été et l'automne et celles dans les eaux profondes (> 200 m) pendant l'hiver et le printemps. De nombreuses femelles ovigères sont revenues l'été suivant dans la région de Grand Manan. Quelques-unes (7 %) se sont déplacées vers le nord sur plus de 30 km pour rentrer dans la baie de Fundy, et vers le sud sur une distance pouvant aller jusqu'à 322 km le long des côtes du Maine. L'examen des données sur les recaptures multiples d'un mois à l'autre a révélé des corrélations positives entre les changements dans la profondeur, la distance parcourue et la température de l'eau. Les migrations saisonnières en profondeur des homards ovigères semblent associées au besoin d'utiliser au mieux les températures qui apportent suffisamment de degrés-jours pour permettre le développement des oeufs. De plus, le fait que les oeufs éclosent dans des eaux relativement chaudes peut conférer un avantage pour la survie des larves pélagiques en diminuant le temps nécessaire pour le passage au stade benthique.

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Knowledge of migratory movements is essential for understanding the relation between the population dynamics, behavior, and environmental requirements of a species. Although directed seasonal deep–shallow migrations are known for the American lobster, *Homarus americanus*, on the continental shelf regions of southern New England and eastern Canada (Saila and Flowers 1968; Cooper and Uzmann 1971, 1980; Uzmann et al. 1977; Fogarty et al. 1980; Campbell et al. 1984), most previous studies indicated that coastal lobsters were nonmigratory with only a few individuals moving long distances (Templeman 1935, 1940a; Wilder 1963; Wilder and Murray 1958; Morrissey 1971; Dow 1974; Cooper et al. 1975; Stasko 1980; Krouse 1980; Campbell 1982). However, recent tagging studies in coastal areas off southwestern Nova Scotia and the Bay of Fundy indicate that some long-distance seasonal migration occurs among mature male and female lobsters (Campbell and Stasko 1985, 1986). Lobsters off the Magdalen Islands (Bergeron 1967; Munro and Therriault 1983) and Newfoundland (Ennis 1984) also have been shown to undergo small-scale depth movements seasonally.

A function for the seasonal shallow–deep migrations of

male and female *H. americanus* has been hypothesized by Cooper and Uzmann (1971, 1980) to supply lobsters on the continental shelf of New England with sufficiently high temperatures to meet the physiological requirements of molting, mating, and egg extrusion. Templeman (1940b) and Perkins (1972) showed that the embryological development rate of *H. americanus* eggs is closely related to temperature. Consequently, the onset of hatching and duration of larval release (few days to several weeks) from ovigerous lobsters can vary between years and between locations, depending on local temperature regimes (Scarratt 1964; Ennis 1975; Harding et al. 1982; Fogarty and Lawton 1983).

The objective of the present study is to provide evidence that seasonal depth migrations by ovigerous *H. americanus* in coastal waters of Grand Manan function to maintain maximum available temperature, thereby providing sufficient degree-days for egg development. Most of the above tagging studies were based on straight-line distances moved based on single release−recapture data which seldom provide an accurate picture of lobster movement. Multiple recapture data are difficult to obtain because normally lobsters are recaptured once and subsequently marketed. In this study, only ovigerous lobsters were tagged. Possession of ovigerous lobsters is prohibited in Canada, so there is an opportunity for multiple recaptures. Such a multiple tagging program can last for about 1 yr because ovigerous females retain their external eggs for 9−12 mo.

## Materials and Methods

Lobsters were caught with baited traps by fishermen throughout the open fishing season (10 November 1982 − 23 June 1983) and during the closed season by fishermen on chartered boats (23 July − 2 November 1982 and 21 July − 26 August 1983) at depths of 5−225 m off the east coast of Grand Manan, New Brunswick. A total of 2139 ovigerous lobsters (85−188 mm CL) (carapace length measured from the base of the eye socket to the posterior margin of the carapace parallel to the mid-dorsal line) were tagged each with a sphyrion anchor tag (Scarratt and Elson 1965; Scarratt 1970), placed into the dorsal musculature between the abdomen and carapace with an hypodermic needle. The coded yellow tubing of the tag protruded dorsally. Tagged ogiverous lobsters were released within 10 min of removal from the water and within 0.5 km of the capture site during July ($N = 3$), August (360), September (650), October (397), November (381), December (47) 1982, January (45), March (9), April (11), May (37), June (173), July (8), and August (18) 1983. Most (66%) of the ovigerous females were captured, tagged, and released in shallow water (<20 m) during July−October 1982 allowing them to disperse before the fishing season began. Tagging additional ovigerous lobsters throughout the experiment period increased the sample size. Only ovigerous lobsters were tagged that had extruded eggs during 1982 and were incubating their eggs during July 1982 − August 1983. Release depth, location, date, tag number, and CL of lobster were recorded. Prior to release, the eggs were categorized as newly extruded (black) or as old (brown with eye spots and/or egg remnants with most eggs hatched). Also, a sample of 10−20 eggs was removed from some lobsters and placed in 5% seawater formalin. All lobsters were tagged and all egg samples were taken by Department of Fisheries and Oceans (DFO) personnel.

To obtain a measure of egg development from the preserved egg samples, the eye index was calculated from the average of the longest and shortest axes of the dark pigmented crescent of an eye of each egg measured to the nearest 0.01 mm (Perkins 1972). The arithmetic mean of 10 measured eggs was used to represent the eye index for each lobster. Overall arithmetic means for monthly samples of lobsters were calculated from the mean eye index of eggs for each lobster.

Water temperatures at various depths off eastern Grand Manan were obtained with reversible thermometers and expendable bathythermographs once a month, and continuous recording thermographs (model J180, Peabody Ryan, Kirkland, WA).

Fishermen were encouraged to leave tags in place when returning recaptured ovigerous lobsters to the sea. A reward of $3 was paid for every tag reported with information provided on recaptured tag number, date, location, and depth. An additional $2 was paid for allowing CL and presence or absence of the egg mass of each tagged lobster to be recorded by DFO personnel. DFO personnel could not be on board all commercial boats during the fishing season; consequently the North Head, Grand Manan, lobster fishermen were provided with vernier calipers and asked to record recapture tag numbers, sex, CL, and presence or absence of eggs. This ensured that the ovigerous lobsters were returned to the water rapidly. A DFO representative collected the information from the fishermen each day. There was over 96% agreement in comparing (1) the CL measured at release and recapture and (2) the locations and depths of each lobster that was recaptured repeatedly within 1 mo by different fishermen and DFO personnel. This verified the accuracy of the recapture information provided by the Grand Manan fishermen. The tagging study also was publicized through posters, news media, and direct contact with fishermen and dealers throughout the Bay of Fundy, southwestern Nova Scotia, and Maine. Information on tag recaptures was obtained through local fisheries observers or by mail. The cooperation of fishermen was excellent. Information reported up to 30 January 1984 is used in this study.

Data on date and location were complete for all recaptures; only 27 recaptures lacked depth information. Straight-line distances and direction traveled were determined from the latitude and longitude of the release and recapture sites using a computer program developed by Campbell et al. (1983). Data were grouped according to (1) time at liberty of six 100-d classes, (2) distance moved from original point of release (≤15, 16−30, 31−50, 51−100, and >100 km), and (3) depth at recapture (≤36, 37−91, 92−182, and >182 m). Data were transformed (unless otherwise indicated) using $\log_{10}(X + 1)$ for distances moved and depth changes per day and $\log_{10}X$ for depth at recapture and time at liberty. Only the geometric means (retransformed means of the logarithmically transformed variables) are shown, unless otherwise indicated.

Two methods were used to investigate the possibility of seasonal trends in recapture depth and distances moved. First, all recaptures (including single or multiple recaptures) were grouped by month, and mean recapture depth and distance moved from the original point of release were calculated. Using two-way analysis of variance (ANOVA) (Kim and Kohout 1975), there were no differences ($p > 0.05$) in distances moved or in depth at recapture between all tagged lobsters released throughout the study period and those tagged and released only during July−October 1982; therefore, all recapture data for each month were combined. Second, only data for lobsters released in one month and recaptured in the next months were

used to indicate mean daily distances moved and depth changes. A depth change was calculated as depth for time $t$ subtracted from depth for time $t + 1$. If lobsters were captured more than once per month, only the information for the last capture for that month was used. All distances moved and depth changes per lobster between months were converted to daily rates by dividing by the number of days at liberty. For each method, differences in mean distance moved or capture depth between monthly periods were compared by a one-way ANOVA and the Student–Newman–Keuls test (Kim and Kohout 1975) after any negative depth changes were converted to positive values and the data transformed as indicated above.

The following equations on the direction of movement for monthly data were computed according to Jones (1959) and Saila and Flowers (1968), using a computer program developed by Campbell et al. (1983).

Mean vector angle:

$$(1)\quad \bar{\theta} = \arctan \frac{\Sigma r \sin \theta}{\Sigma r \cos \theta}.$$

Mean square dispersion coefficient (square kilometres per day):

$$(2)\quad a^2 = \frac{1}{n}\left[\sum \frac{r^2}{t} - \frac{(\Sigma\, r \cos \theta)^2 + (\Sigma\, r \sin \theta)^2}{\Sigma t}\right]$$

North–south direction component (kilometres per day):

$$(3)\quad V = \frac{\Sigma r \cos \theta}{\Sigma t}.$$

East–west direction component (kilometres per day):

$$(4)\quad V' = \frac{\Sigma r \sin \theta}{\Sigma t}.$$

Rayleigh test:

$$(5)\quad Z = R^2/n$$

where $n$ = number of individual tag returns,

$$R = \sqrt{(\Sigma \sin \theta)^2 + (\Sigma \cos \theta)^2},$$

$r$ = apparent "straight-line" distance traveled (kilometres) from release to recapture point, $\theta$ = angle of direction of travel based on deviation from true north, and $t$ = time (days) from release to recapture. The Rayleigh test is a test for randomness of distribution of points about a circle (Batschelet 1965). The mean square dispersion coefficient is dependent on the rate of travel and as the mean distance traveled and is a measure of random movement based on physical theories of diffusion and heat conduction (Skellam 1951; Jones 1959). The parameters $V$ and $V'$ indicate the mean rate of directed (nonrandom) movement of a group of tagged lobsters in the north–south and east–west direction, respectively.

The relationships between depth, distance, and temperature changes between months were examined using the linear regression equations

$$(6)\quad D' = a + bT'$$

$$(7)\quad D = a + bM$$

and the multiple regression equation

$$(8)\quad D = a + bM + cT$$

where $D$ and $D'$ = depth change per day, $M$ = distance moved per day, and $T$ and $T'$ = temperature change between months (using July–October 1982 and July–August 1983 surface temperatures and November 1982 – June 1983 bottom temperatures), and $a$, $b$, and $c$ are constants estimated with a simple linear and a multiple regression program (Kim and Kohout 1975) after variables $D$ and $M$ were $\log_{10}(X + 1)$ transformed. Since all values of $M$ were positive, negative depth ($D$) and temperature ($T$) changes were converted to positive values prior to transformation of $D$ and $M$ for equations 7 and 8. Only the untransformed data (including negative values) for variables $D'$ and $T'$ were used in equation 6.

Movement data obtained from the recovery of tagged lobsters provided by commercial fishermen should be considered with caution because bias can be introduced by the nonuniform distribution of fishing effort. The ideal situation in which fishing effort is distributed uniformly in both space and time usually is never achieved for tagging studies (e.g. see discussions by Fogarty et al. 1980; Bennett and Brown 1983; Diamond and Hankin 1985). In this study, although fishing effort usually was concentrated in areas and depths where lobster densities were high, exploratory traps were placed in areas which were marginally profitable. Consequently, the extensive trap distribution should have approximated the distribution of lobsters. Traps were placed at most depths of water near Grand Manan throughout the year by fishermen during the fishing season and by a chartered boat during the closed season. In addition, the fishing season in Maine is open all year although the highest effort occurs from May to October (Thomas 1973). The catchability of lobsters with baited traps will depend on the lobsters feeding activity, and thus, during periods of molting and low temperature, the probability of capture is reduced (McLeese and Wilder 1958; Elner 1980). SCUBA diving in 5- to 10-m waters near North Head, Grand Manan, indicated concentrations of ovigerous lobsters during August 1982 and 1983, whereas none were seen during December 1982 (A. Campbell, unpubl. data). Although the exact catchability of females in different reproductive conditions was not known, this was probably not a major problem, since many mature males and ovigerous and nonovigerous females were caught in the baited traps set by fishermen in the Grand Manan area throughout 1982–83. Also, traps were designed to be nonselective for mature lobsters >94 mm CL (Campbell and Duggan 1980). Although the rate of tag loss during molting and/or mortality due to poor tag application was unknown, individuals applying tags to lobsters were well trained and experienced so that tag loss was considered minimal.

## Results

Of the 2139 ovigerous lobsters tagged and released, 1046 (48.9%) individual lobsters were recaptured. There was, however, a total of 1877 single and multiple recaptures. Of the 1046 individuals recaptured, 589 (56.3%) were caught once, 245 (23.4%) twice, 123 (11.8%) three, 49 (4.7%) four, 20 (1.9%) five, 12 (1.1%) six, 5 (0.5%) seven, 2 (0.2%) eight, and 1 (0.1%) 10 times.

### Time at Liberty

Most lobsters (67%) were captured within 100 d; the percentage returns generally decreased with increased time at liberty (Fig. 1A).

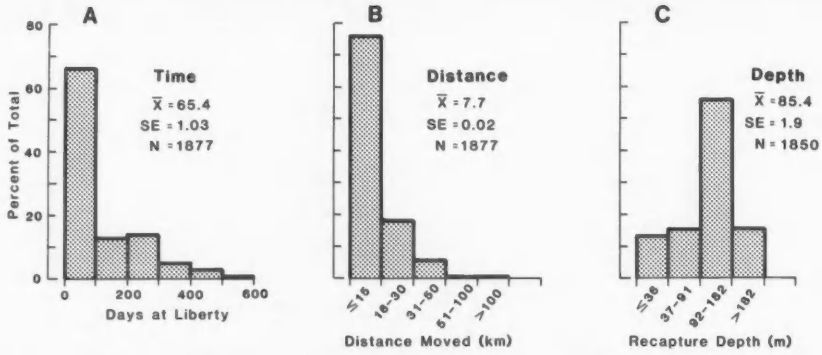


FIG. 1. Percentage of total recaptures of tagged ovigerous lobsters off Grand Manan, 1982–83, by (A) days at liberty, (B) distance moved, and (C) recapture depth. $\bar{X}$ = geometric mean; SE = standard error; $N$ = number of single and multiple recaptures combined.

TABLE 1. Direction statistics by month for tagged ovigerous lobsters off Grand Manan, 1982–83. $\bar{\theta}$ = mean vector angle from true north; $a^2$ = mean square dispersion coefficient; $V$ and $V'$ = nonrandom movement along north–south and east–west planes, respectively; negative values of $V$ and $V'$ = net southerly and westerly movement, respectively; $R$ and $Z$ = Rayleigh test statistics for randomness of distribution of points about a circle; * = significant at $p < 0.01$, indicating a nonuniform distribution (Batschelet 1965); $N$ = sample size.

| Month of release | Month of recapture | $\bar{\theta}$ | $a^2$ (km²/d) | $V$ (km/d) | $V'$ (km/d) | $R$ | $Z$ | $N$ |
|---|---|---|---|---|---|---|---|---|
| August 1982 | September 1982 | 341 | 0.01 | 0.003 | −0.001 | 48.0 | 47.0* | 49 |
| September | October | 125 | 0.1 | −0.018 | 0.025 | 24.8 | 14.7* | 42 |
| October | November | 83 | 2.6 | 0.024 | 0.186 | 105.1 | 77.3* | 143 |
| November | December | 143 | 6.3 | −0.198 | 0.150 | 80.3 | 45.1* | 143 |
| December 1982 | January 1983 | 130 | 14.2 | −0.306 | 0.368 | 24.7 | 16.5* | 37 |
| January 1983 | February 1983 | 43 | 9.9 | 0.046 | 0.043 | 1.7 | 0.4 | 7 |
| April | May | 214 | 1.2 | −0.012 | −0.008 | 2.0 | 0.7 | 6 |
| May | June | 339 | 10.8 | 0.182 | −0.071 | 14.7 | 6.0* | 36 |
| June | July | 322 | 11.4 | 0.185 | −0.147 | 5.0 | 4.2* | 6 |
| July | August | 270 | 0.2 | 0.000 | −0.058 | 1.5 | 0.8 | 3 |

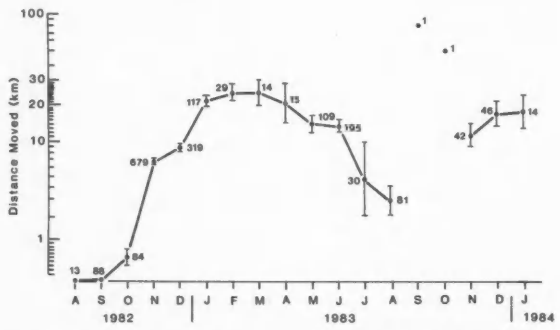


FIG. 2. Mean straight-line distance moved from original release point grouped by month for ovigerous lobsters tagged off Grand Manan, 1982–83. Points are geometric means; vertical bars are 95% confidence intervals; number by each point is the number of single and multiple recaptures combined.

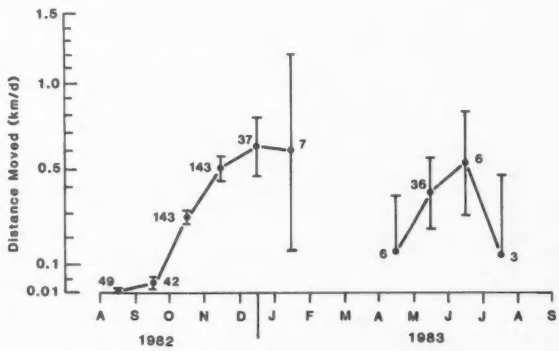


FIG. 3. Mean straight-line distance moved per day for tagged ovigerous lobsters released in one month and captured the next month off Grand Manan, 1982–83. Points are geometric means; vertical bars are 95% confidence intervals; number by each point is the number of individuals.

## Distance Moved

Most lobsters (75%) were recaptured <15 km from the release sites (Fig. 1B). However, seasonal comparisons indicated that lobsters were furthest (>20 km) away (ANOVA, $p <$ 0.01) during winter (January–March) 1983 compared with those caught (<10 km) during summer–fall (August–December) 1982 and summer (July–August) 1983 (Fig. 2). There were two movement activity peaks during December

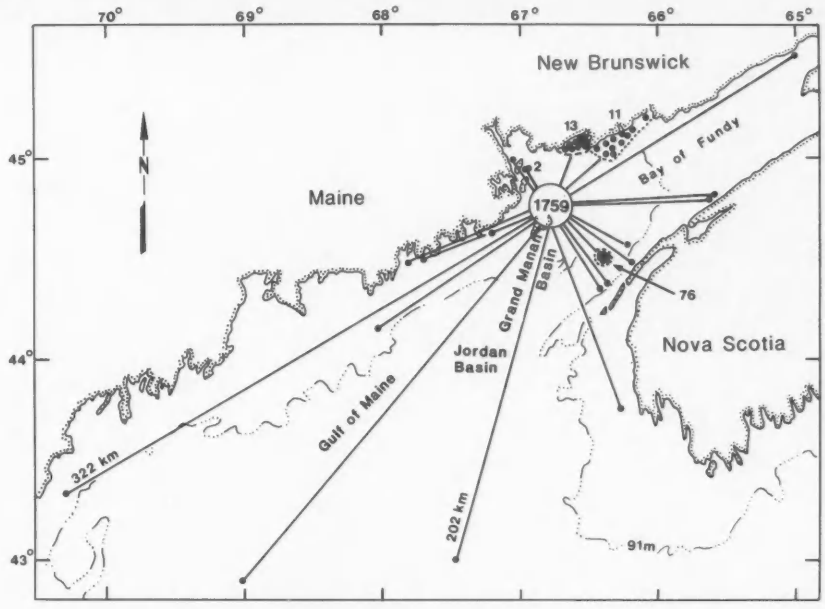


FIG. 4. Recapture points and straight-line distances moved by tagged ovigerous lobsters released off Grand Manan, 1982–83. Each point represents one recapture except where otherwise shown. Number in circle is the number of recaptured lobsters that moved <30 km.

1982 – January 1983 and during June–July 1983 (Fig. 3). This agrees with the peaks in dispersal activity shown by the calculated mean square dispersion coefficient $a^2$ (Table 1). The fastest rate of individual movement recorded was 3.1 km/d for a 139 mm CL lobster at liberty for 66 d. The longest straight-line movement was 322 km for a 136 mm CL lobster at liberty for 329 d (Fig. 4.)

## Directional Movement

Examination of the straight-line distances between release and recapture points of the few lobsters (7%) that moved >30 km indicates some movement of lobsters within the whole of the Bay of Fundy and the Gulf of Maine (Fig. 4). More detailed patterns of movement were observed for the 457 lobsters that were recaptured more than once, e.g. in Fig. 5. During fall, the multiple tag returns indicated that lobsters moved north and/or east from Grand Manan into deeper waters, occasionally remained in an area and/or moved in various directions but staying at the same depth. Subsequently, the lobsters moved further south and deeper into the Grand Manan Basin (Fig. 5). Little information is available on the location of most of the ovigerous lobsters, since few were caught by traps and/or fish trawls (A. Campbell, unpubl. data) during January–April 1983. However, assuming that the ovigerous females were in the Grand Manan Basin or Jordan Basin during winter 1983, then the direction of travel for the lobsters returning to the shallow waters of Grand Manan during summer 1983 would be northwest. The directional statistics (Table 1) confirm that there were significant directed movements by lobsters south and east away from Grand Manan during September 1982 – January 1983 and directed movements north and west back to Grand Manan during May–July 1984. During January–February and April–May 1983, there were no significant directed movements, with the Rayleigh tests indicating a uniform distribution although the sample sizes were small (Table 1).

## Recapture Depth

The majority (56%) of females were recaptured at 92- to 182-m depths (Fig. 1C). The shallowest and deepest recaptures were 5 and 225 m. Lobsters moved to deeper water during fall 1982, remained in deep water during January–June 1983, and returned to shallow water during July–September 1983 (Fig. 6). The peak activities in depth change were to deeper waters (positive) during November 1982 – January 1983 and to shallow waters (negative) during July 1983 (Fig. 7).

## Temperature Trends

Temperature of shallow water was higher during summer and lower during winter than for deep (182 m) water near Grand Manan (Fig. 8).

## Depth–Distance–Temperature Relation

Depth changes by lobsters per day ($D'$) were correlated with water temperature change between months ($T'$) (untransformed data and negative values used):

$$D' = -0.027 - 0.950T'$$
$$(R = -0.47;\ p < 0.01;\ \text{SE} = 2.11;\ N = 469).$$

The daily change in depth ($D$) also was correlated with distance moved ($M$) (after $\log_{10}(X + 1)$ transformation):

$$D = 0.190 + 1.369M$$
$$(R = 0.57;\ p < 0.01;\ \text{SE} = 0.22;\ N = 469).$$

A multiple regression of the three variables also was signifi-

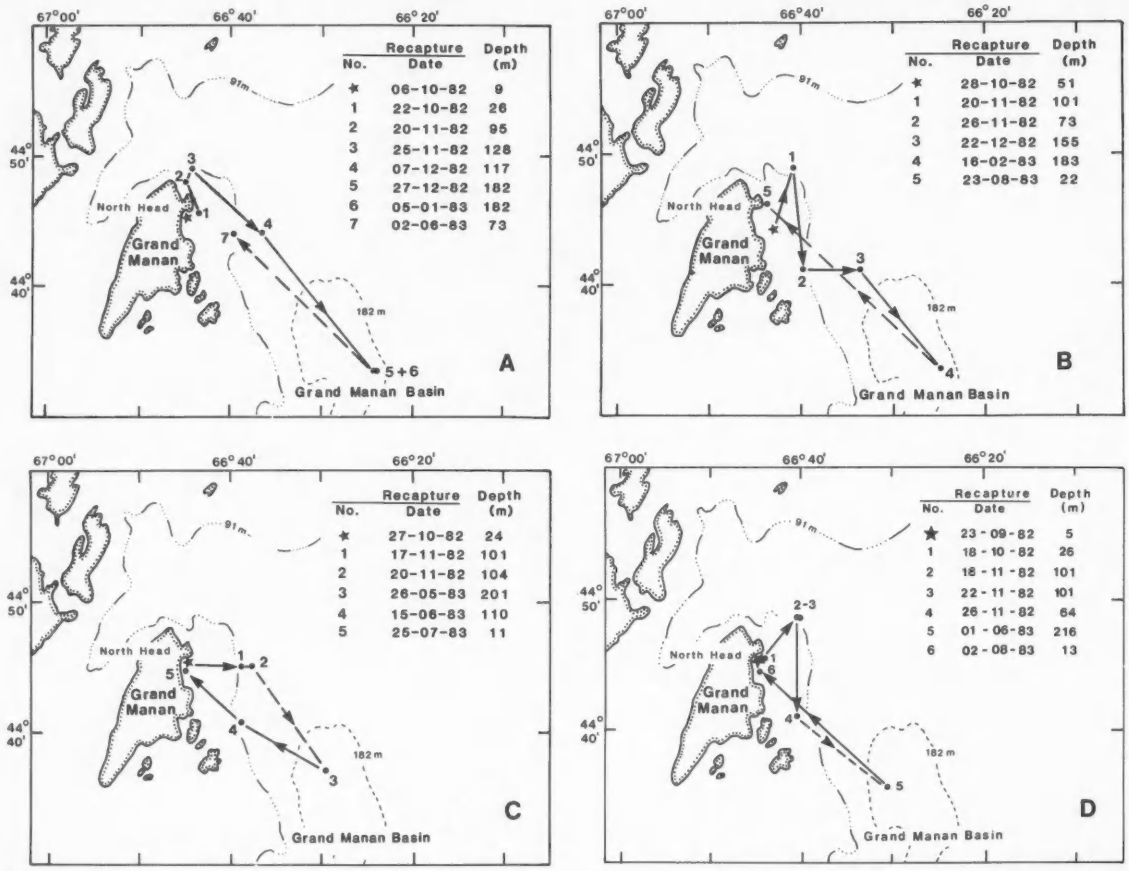


FIG. 5. Multiple recapture of each of four tagged ovigerous females (A) 133 mm CL, (B) 109 mm CL, (C) 135 mm CL, and (D) 131 mm CL released near Grand Manan, September–October 1982. Asterisks and points indicate release and recapture locations; broken line indicates >3 mo between recaptures.

cant (negative values of $D$ and $T$ were made positive and $D$ and $M$ were $\log_{10}(X + 1)$ transformed):

$$D = -0.123 + 1.067M + 0.222T$$
$$(R = 0.72;\ \text{df} = 2{,}466;\ F = 246;\ p < 0.01;\ \text{SE} = 0.19).$$

The daily distance moved had a similar positive influence ($\beta = 0.45$) as temperature ($\beta = 0.44$) on depth change.

## Egg Development

In the Grand Manan area, egg extrusion occurs between July and October and extrusion peaks in mid-August – late September (Fig. 9). The eggs hatch into pelagic larvae the following July–September with peak hatching occurring during the last half of August. Mature females usually remain non-ovigerous for about 1 yr after hatching eggs (Aiken and Waddy 1980; Campbell 1983).

The development of lobster eggs is illustrated by the eye indices for 1982–83 in Fig. 10. The eggs developed rapidly from September to December when bottom water temperatures were high (7–12°C, Fig. 8); egg development was slowed during January–June at lower temperatures (1–6°C). Subsequently, development rate increased during July–August at the higher temperatures (7–12°C). The mean eye index value for August 1983 appeared to be reduced, possibly because larvae had already hatched from the eggs of some lobsters leaving only lobsters with less-developed eggs to be sampled. Perkins (1972) considered an eye index of 560 μm to be a value at which larvae hatch from eggs. In the present study, the maximum eye indices recorded for July and August 1983 were 561 and 571 μm, respectively.

The following calculations suggest that an ovigerous lobster needs to make seasonal deep–shallow water migrations to obtain sufficient heat units for complete egg development within a 9- to 12-mo period. Using lobster egg development rates at different constant temperatures, provided by Perkins (1972), the method of Campbell et al. (1974) was used to calculate a threshold temperature for development of 3.4°C and degree-days required from egg extrusion to larval hatch of approximately 1832. The number of degree-days above 3.4°C was calculated (Table 2) from the seasonal temperature regimes (Fig. 8). There were insufficient degree-days for complete egg development if a female remained either at the shallow or deep areas all year. During November–June, the deep water had 88 degree-days more than shallow water. During August–October 1982 and July–August 1983, shallow water had 351 degree-days more than deep water (Table 2). By adding the

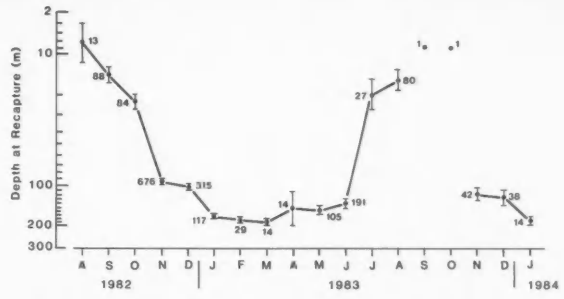


FIG. 6. Mean depth at recapture grouped by month for ovigerous lobsters tagged off Grand Manan, 1982–83. Points are geometric means; vertical bars are 95% confidence intervals; number by each point is the number of single and multiple recaptures.

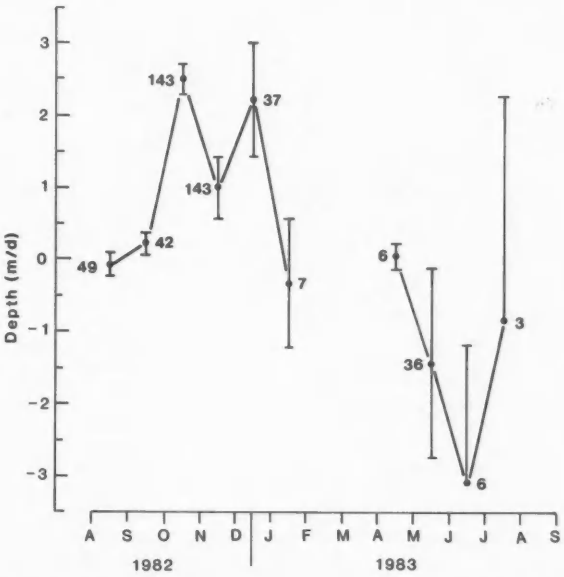


FIG. 7. Mean depth change per day for tagged ovigerous lobsters released in one month and recaptured the next month off Grand Manan, 1982–83. Points are arithmetic means; vertical bars are 95% confidence intervals; number by each point is the number of individuals recaptured in 1 mo.

summer and fall shallow-water and the winter deepwater degree-days, there are enough heat units for complete egg development within about 1 yr (Table 2).

## Discussion

This study shows that ovigerous *H. americanus* females in the Grand Manan area undergo seasonal deep–shallow water migrations, maintaining the lobsters at the highest local water temperature. The multiple recapture data show that although some ovigerous lobsters were caught a short distance (<1 km) from the original release location after 1 yr at liberty, they had made round-trip movements of >20 km. The measurement of this seasonal depth migration is thus better shown by depth at recapture and multiple tag recaptures than by single recaptures

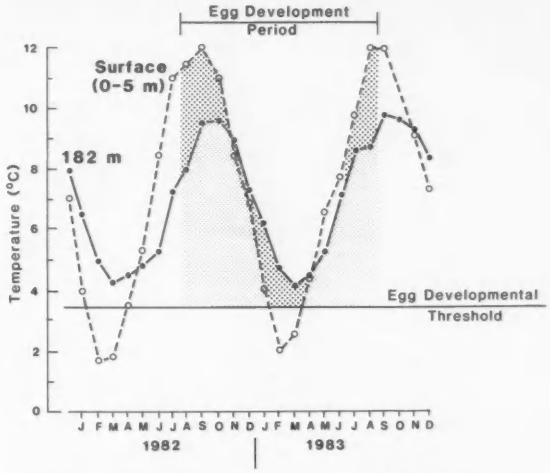


FIG. 8. Seasonal surface and deepwater (182 m) temperatures off Grand Manan, 1982–83. The lobster egg developmental temperature threshold is calculated from Perkins (1972). Stippled areas are the heat units available above the threshold temperature; dark stippled areas indicate extra heat units obtained as a consequence of the seasonal migration of ovigerous lobsters.

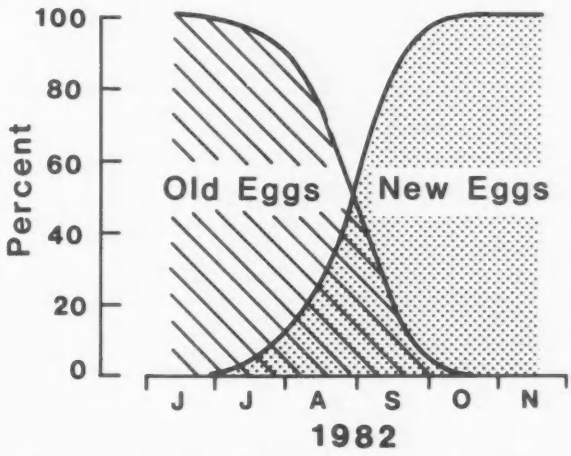


FIG. 9. Percentage of old eggs (larvae about to hatch) and newly extruded eggs on ovigerous lobsters examined off Grand Manan, 1982. About 100 ovigerous lobsters were examined per week and eggs were categorized visually as old or new.

of lobsters at liberty for long periods (>3 mo). The multiple and depth at recapture data show that there are two peaks of migratory activity in ovigerous females in a year. The first peak occurs during fall when the lobsters move south and east >30 km, going from depths of about 5 m to >200 m. The second movement when they return to shallow water occurs during June–July. Although some lobsters return to the same area, others may move to the northeast into the Bay of Fundy, west to the Maine coastline, or south to shoal water of the continental shelf (see also Campbell and Stasko 1986).

Although changes in temperature, daily distance moved, and depth by lobsters were correlated significantly, the constants

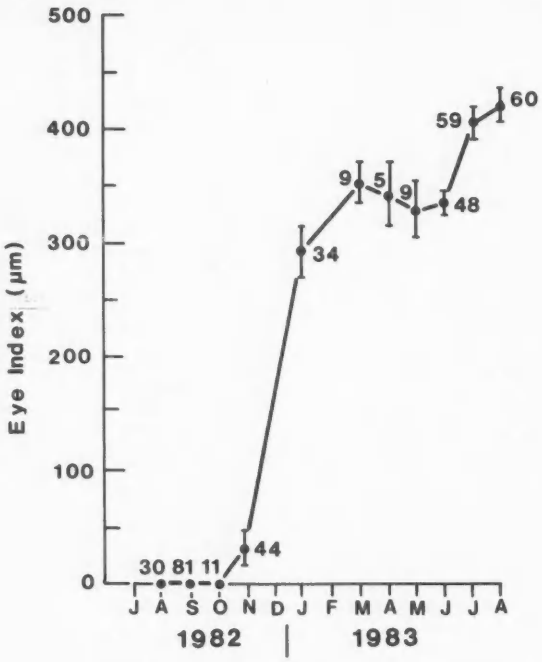


FIG. 10. Monthly mean lobster egg eye index indicating egg development for ovigerous lobsters sampled off Grand Manan during the 1982–83 developmental period. Points are arithmetic means; vertical lines are 95% confidence intervals; number by each point is the number of lobsters sampled.

for the linear and multiple regression equations generated in this study probably are influenced by the local bottom topography and only applicable to the specific area. The seabed east of Grand Manan slopes rapidly into deep water and lobsters do not need to move far to shallow or deep water (Fig. 5). Campbell and Stasko (1986) found that for the upper reaches of the Bay of Fundy, the seabed slope is gradual and lobsters must move further to reach deep water (Fig. 4). Such a temperature-dependent seasonal migration can explain some of the long- and short-distance movements of lobsters (Campbell and Stasko 1986), although it may not be a well-coordinated phenomenon, since some lobsters may move laterally along the slopes of the continental shelf (Cooper and Uzmann 1980; Pezzack and Duggan 1986).

There is no clear understanding of the endogenous and external factors that control seasonal migrations in *H. americanus*. Several large marine decapods undergo migrations and fulfill a variety of biological functions such as avoiding predators, finding mates, ovary maturation, care of offspring, and improving larval recruitment (see reviews by Allen 1966; Herrnkind 1980, 1983; Rebach 1983, 1985; more recent examples of breeding migrations in crabs are reported by Bennett and Brown 1983; Dittel et al. 1985; Sloan 1985; Taylor et al. 1985). Some spiny lobster species show migrations associated with breeding and release of larvae close to oceanic currents which allow for favorable distribution of larvae to juvenile nursery areas, e.g. *Panulirus ornatus* undertakes a mass migration across the Gulf of Papua to spawning grounds (Moore and MacFarlane 1984; MacFarlane and Moore 1986) and *Jasus verreauxi* migrates

TABLE 2. Degree-days (above threshold temperature of 3.4°C for egg development) calculated from water temperature records near Grand Manan during the 1982–83. Degree-days required for complete egg development estimated to be 1832 from Perkins (1972).

| Dates | Degree-days | |
|---|---|---|
| | Shallow water (0–5 m) | Deep water (182 m) |
| August 1982 – October 1982 | 745[a] | 515 |
| November 1982 – June 1983 | 532 | 620[a] |
| July 1983 – August 1983 | 462[a] | 341 |
| Total | 1739 | 1476 |

[a]Combined degree-days = 1827.

contranatantly to breed off northern New Zealand (Booth 1986). Although migrations by adult *H. americanus* can be related to reproduction, they probably are connected more with temperature changes than with contranatant movements; indeed there is no clear link between the locations of larval release and settlement (Ennis 1986; Campbell and Pezzack 1986).

For *H. americanus*, the seasonal depth migrations are associated with maximizing degree-days needed for molting, growth, gonad development, egg extrusion (Cooper and Uzmann 1971, 1980), and egg development (this study; Campbell and Stasko 1986). Examination of the local temperatures (Fig. 8) suggests that the movement of ovigerous females into warm shallow water in summer results in their eggs hatching during a period when surface temperature is high. This behavior may confer a survival advantage for the pelagic larvae by decreasing developmental time from larval hatch to the benthic stage (Templeman 1936) and thus enhancing the probability of larval survival (Huntsman 1923; Caddy 1979).

## Acknowledgments

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## References

AIKEN, D. E., AND S. L. WADDY. 1980. Reproductive biology of lobsters, p. 215–276. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 1. Academic Press, New York, NY. 463 p.

ALLEN, J. A. 1966. The rhythms and population dynamics of decapod Crustacea. Oceanogr. Mar. Biol. Annu. Rev. 4: 247–265.

BATSCHELET, E. 1965. Statistical methods for the analysis of problems in animal orientation and certain biological rhythms. American Institute of Biological Sciences, Arlington, VA. 54 p.

BENNETT, D. B., AND C. G. BROWN. 1983. Crab (*Cancer pagurus*) migrations in the English Channel. J. Mar. Biol. Assoc. U.K. 63: 371–398.

BERGERON, J. 1967. Contribution à la biologie du homard (*Homarus americanus*) des Iles-de-la Madeleine. Naturaliste Can. (Que.) 94: 169–207.

BOOTH, J. D. 1986. Recruitment of packhorse rock lobster *Jasus verreauxi* in New Zealand. Can. J. Fish. Aquat. Sci. 43: 2212–2220.

CADDY, J. F. 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 1975: 204–216.

CAMPBELL, A. 1982. Movements of tagged lobsters released off Port Maitland, Nova Scotia, 1944–80. Can. Tech. Rep. Fish. Aquat. Sci. 1136: 41 p.

1983. Growth of tagged American lobsters, *Homarus americanus*, in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 40: 1667–1675.

CAMPBELL, A., S. E. BELLIS, G. E. FAWKES, AND C. HASTEY. 1983. Computer programs for analysis of lobster (*Homarus americanus*) movements from tag–recapture data. Can. MS Rep. Fish. Aquat. Sci. 1705: 22 p.

CAMPBELL, A., AND D. R. DUGGAN. 1980. Review of the Grand Manan lobster fishery with an analysis of recent catch and effort trends. Can. Tech. Rep. Fish. Aquat. Sci. 997: 20 p.

CAMPBELL, A., D. B. FRAZER, N. GILBERT, A. P. GUTIERREZ, AND M. MACKAUER. 1974. Temperature requirements of some aphids and their parasites. J. Appl. Ecol. 11: 431–438.

CAMPBELL, A., D. E. GRAHAM, H. J. MACNICHOL, AND A. M. WILLIAMSON. 1984. Movements of tagged lobsters released on the continerntal shelf from Georges Bank to Baccaro Bank, 1971–73. Can. Tech. Rep. Fish. Aquat. Sci. 1288: 16 p.

CAMPBELL, A., AND D. S. PEZZACK. 1986. Relative egg production and abundance of berried lobsters, *Homarus americanus*, in the Bay of Fundy and off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 2190–2196.

CAMPBELL, A., AND A. B. STASKO. 1985. Movements of tagged American lobsters, *Homarus americanus*, off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 42: 229–238.

1986. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. Mar. Biol. (In press)

COOPER, R. A., R. A. CLIFFORD, AND C. D. NEWELL. 1975. Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay region of Maine. Trans Am. Fish. Soc. 104: 669–674.

COOPER, R. A., AND J. R. UZMANN. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science (Wash., DC) 171: 288–290.

1980. Ecology of juvenile and adult *Homarus*, p. 97–142. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

DIAMOND, N., AND D. G. HANKIN. 1985. Movements of adult female Dungeness crabs (*Cancer magister*) in northern California based on tag returns. Can. J. Fish. Aquat. Sci. 42: 919–926.

DITTEL, A. I., C. E. EPIFANIO, AND J. B. CHAVARRIA. 1985. Population biology of the portunid crab *Callinectes arcuatus* Ordway in the Gulf of Nicoya, Costa Rica, Central America. Estuarine Coastal Shelf Sci. 20: 593–602.

DOW, R. L. 1974. American lobsters tagged by Maine commercial fishermen, 1957–59. Fish. Bull. U.S. 72: 622–623.

ELNER, R. W. 1980. Lobster gear selectivity — a Canadian overview. Can. Tech. Rep. Fish. Aquat. Sci. 932: 77–83.

ENNIS, G. P. 1975. Observations on hatching and larval release in the lobster *Homarus americanus*. J. Fish. Res. Board Can. 32: 2210–2213.

1984. Small-scale seasonal movements of the American lobster *Homarus americanus*. Trans. Am. Fish. Soc. 113: 336–338.

1986. Stock definition, recruitment variability, and larval recruitment processes in the American lobster, *Homarus americanus*: a review. Can. J. Fish. Aquat. Sci. 43: 2072–2094.

FOGARTY, M. J., D. V. D. BORDEN, AND H. J. RUSSELL. 1980. Movements of tagged American lobster, *Homarus americanus*, off Rhode Island. Fish. Bull. U.S. 78: 771–780.

FOGARTY, M. J., AND R. LAWTON. 1983. An overview of larval American lobster, *Homarus americanus*, sampling programs in New England during 1974–79. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-775: 9–14.

HARDING, G. C., W. P. VASS, AND K. F. DRINKWATER. 1982. Aspects of larval American lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia. Can. J. Fish. Aquat. Sci. 39: 1117–1129.

HERRNKIND, W. F. 1980. Spiny lobsters: patterns of movement, p. 349–407. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 1. Academic Press, New York, NY. 463 p.

1983. Movement patterns and orientation, p. 41–105. *In* P. E. Bliss [ed.] The biology of crustacea. Vol. 7. Academic Press, New York, NY.

HUNTSMAN, A. G. 1923. Natural lobster breeding. Bull. Biol. Board Can. 5: 1–11.

JONES, R. 1959. A method of analysis of some tagged haddock returns. J. Cons. Int. Explor. Mer 25: 58–72.

KIM, J.-O., AND F. J. KOHOUT. 1975. Analysis of variance and covariance: subprograms ANOVA and ONEWAY, p. 398–433. *In* N. H. Nie, C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent [ed.] Statistical package for the social sciences. McGraw-Hill Book Co., New York, NY. 675 p.

KROUSE, J. S. 1980. Summary of lobster, *Homarus americanus*, tagging studies in American waters (1898–1978). Can. Tech. Rep. Fish. Aquat. Sci. 932: 135–140.

MACFARLANE, J. W., AND R. MOORE. 1986. Reproduction of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. Aust. J. Mar. Freshwater Res. 37: 55–65.

MCLEESE, D. W., AND D. G. WILDER. 1958. The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. J. Fish. Res. Board Can. 15: 1345–1354.

MOORE, R., AND J. W. MACFARLANE. 1984. Migration of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. Aust. J. Mar. Freshwater Res. 35: 197–212.

MORRISSEY, T. D. 1971. Movements of tagged American lobsters, *Homarus americanus*, liberated off Cape Cod, Massachusetts. Trans. Am. Fish. Soc. 100: 117–120.

MUNRO, J., AND J.-C. THERRIAULT. 1983. Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des Îles-de-la-Madeleine. Can. J. Fish. Aquat. Sci. 40: 905–918.

PERKINS, H. C. 1972. Development rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). Fish. Bull. U.S. 70: 95–99.

PEZZACK, D. S., AND D. R. DUGGAN. 1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. 43: 2206–2211.

REBACH, S. 1983. Orientation and migration in Crustacea, p. 217–264. *In* S. Rebach and D. W. Dunham [ed.] Studies in adaptation, the behavior of higher crustacea. John Wiley & Sons, New York, NY.

1985. Rhythmicity under constant conditions in the rock crab, *Cancer irroratus*. Bull. Mar. Sci. 36: 454–466.

SAILA, S. B., AND J. M. FLOWERS. 1968. Movements and behaviour of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. J. Cons. Int. Explor. Mer 31: 342–351.

SCARRATT, D. J. 1964. Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. J. Fish. Res. Board. Can. 21: 661–680.

1970. Laboratory and field tests of modified sphyrion tags on lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 27: 257–264.

SCARRATT, D. J., AND P. F. ELSON. 1965. Preliminary trials of a tag for salmon and lobsters. J. Fish. Res. Board Can. 22: 421–423.

SKELLAM, J. G. 1951. Random dispersal in theoretical populations. Biometrika 38: 196–218.

SLOAN, N. A. 1985. Life history characteristics of fjord-dwelling golden king crabs *Lithodes aequispina*. Mar. Ecol. Prog. Ser. 22: 219–228.

STASKO, A. B. 1980. Tagging and lobster movements in Canada. Can. Tech. Rep. Fish. Aquat. Sci. 932: 141–150.

TAYLOR, D. M., R. G. HOOPER, AND G. P. ENNIS. 1985. Biological aspects of the spring breeding migration of snow crabs, *Chionoecetes opilio*, in Bonne Bay, Newfoundland (Canada). Fish. Bull. U.S. 83: 707–711.

TEMPLEMAN, W. 1935. Lobster tagging in the Gulf of St. Lawrence. J. Biol. Board. Can. 1: 269–278.

1936. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J. Biol. Board Can. 2: 485–497.

1940a. Lobster tagging on the west coast of Newfoundland 1938. Nfld. Dep. Nat. Resour. Fish. Res. Bull. 8: 16 p.

1940b. Embryonic developmental rates and egg-laying of Canadian lobsters. J. Fish. Res. Board Can. 5: 71–83.

THOMAS, J. C. 1973. An analysis of the commercial lobster (*Homarus americanus*) fishing along the coast of Maine, August 1966 through December 1970. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-667.

UZMANN, J. R., R. A. COOPER, AND K. J. PECCI. 1977. Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the southern New England continental shelf. U.S. Dep. Commer. NOAA Tech. Rep NMFS SSRF-705: 92 p.

WILDER, D. G. 1963. Movements, growth and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. J. Fish. Res. Board Can. 20: 305–318.

WILDER, D. G., AND R. C. MURRAY. 1958. Do lobsters move offshore and onshore in the fall and spring? Fish. Res. Board Can. Atl. Prog. Rep. 69: 12–15.

# Evidence of Migration and Homing of Lobsters (*Homarus americanus*) on the Scotian Shelf

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Pezzack, D. S., and D. R. Duggan. 1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. 43: 2206–2211.

In the Browns Bank region of the Scotian Shelf between June 1982 and December 1983, 6285 tagged lobsters (*Homarus americanus*) were released. Of the 2486 lobsters recaptured, 361 were recaptured more than once. Eight lobsters released in late May to mid-July were recaptured the following spring and summer, with at least one intervening recapture in the fall–winter period. Five of the eight lobsters showed homing tendencies. Two lobsters made long-distance (>200 km) return migrations, three made short (50–100 km) return migrations, and three moved long distances but did not return. One lobster at large 6 mo and four at large 22–34 mo made long-distance return migrations, moving over 200 km and returning to within 9–42 km of the initial release site. The data indicate that some lobsters undertake long-distance return migration, which returns the lobsters to specific sections of the Shelf.

Sur le plateau continental Scotian, dans la région du banc de Browns, entre juin 1982 et décembre 1983, on a libéré 6 285 homards (*Homarus americanus*) marqués. Sur les 2 486 homards qui ont été recapturés, 361 l'ont été plus d'une fois. Huit homards libérés entre la fin mai et la mi-juillet ont été recapturés au cours du printemps et de l'été suivants, avec au moins une recapture entre temps pendant la période automne–hiver. Cinq des huit homards montraient des tendances à revenir sur leur lieu de naissance. Deux homards ont effectué des migrations de retour sur de longues distances (>200 km), trois des migrations courtes (50–100 km) et trois se sont déplacés sur de grandes distances mais ne sont pas revenus. Un homard parti pendant 6 mois et quatre homards partis pendant 22 à 34 mois ont effectué de longues migrations de retour, parcourant plus de 200 km et revenant à une distance de 9 à 42 km du point de libération. Les données indiquent que certains homards entreprennent de longues migrations de retour qui les ramènent en des points précis du plateau continental.

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Knowledge of the migratory movements of the American lobster (*Homarus americanus*, Milne-Edwards) is essential for an understanding of lobster stock relationships, population, and fishery dynamics. Long-term studies of lobster movement became possible in the late 1960's with the use of the sphyrion tag (Scarratt and Elson 1965) for lobster. The tag is retained through the molt. Numerous tagging programs have been undertaken to study lobster movements in Georges Bank (Cooper and Uzmann 1971; Uzmann et al. 1977; Campbell et al. 1984), Gulf of Maine (Morrissey 1971; Dow 1974; Krouse 1980; Campbell 1982), and Scotian Shelf regions (Stasko 1980; Campbell et al. 1984; Campbell and Stasko 1985).

Little is known of the relationship between concentrations of lobster in the shallow coastal areas and deepwater (100–600 m) offshore areas in the Gulf of Maine and on the adjacent continental shelf and slope (Pezzack 1984). Analyses of the seasonal changes in the recapture depth of tagged lobsters suggest that some undertake movements in late spring from the upper continental slope to shallow areas of Georges Bank (Cooper and Uzmann 1971; Uzmann et al. 1977) and the outer Scotian Shelf (Campbell et al. 1984) and return to deep water in winter. The annual movements of individual lobsters have not been followed and it is not known if lobsters return to the same area or "home" territory on the return movement or if the movements are simply seasonal wanderings of a nomadic nature in response to temperature changes (Cooper and Uzmann 1980). Herrnkind (1980) defined migration as the directed movement of a population (or a distinct component of the population) within a confined time period over a long distance. The definition does not require return movement. Return migrations, which bring the lobsters back to a site or area previously visited, represent a special case and are distinguished from exploratory and removal migration (Steen 1984).

Saila and Flowers (1968) and Fogarty et al. (1980) showed that lobsters caught on the continental slope and moved to and released in coastal or midshelf regions moved toward the continental slope, and in some cases returned to areas near the original capture site. Many studies of lobsters in coastal regions suggest that they are nonmigratory, undertaking only small-scale movements (Wilder 1963; Krouse 1980, 1981; Stasko 1980; Campbell 1982; Ennis 1984). There are indications that large, mature lobsters may undertake long-distance and seasonal migrations (Krouse 1980; Campbell 1984) similar to those observed in offshore regions.

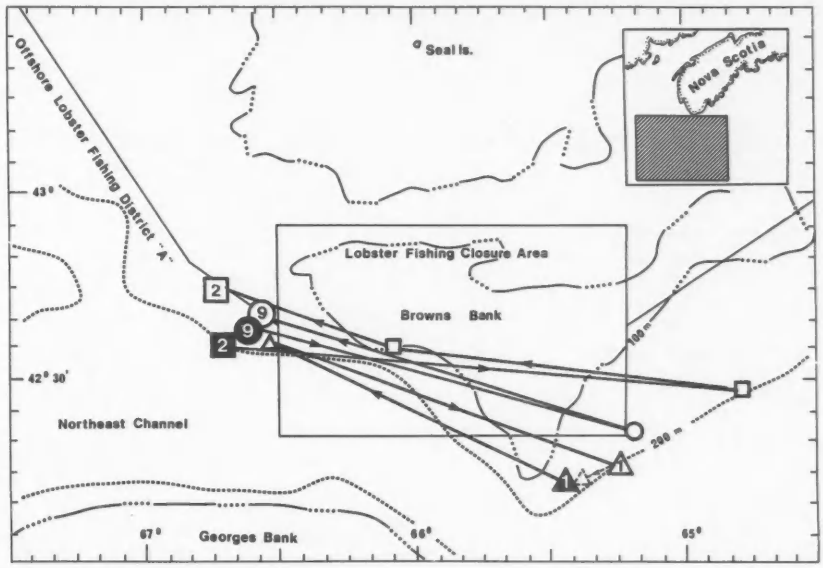


FIG. 1. Tagging locations (▲, ■, ●) and intermediate (△, □, ○) and final (△, □, ○) recapture sites of lobsters at large 10−14 mo (lobsters 1 and 2) and <10 mo (lobster 9) which undertook long-distance (>100 km) return movements (see Table 1 for dates and distances).

In the majority of tagging studies, most of the lobsters are recaptured after a short time (<2 mo) and close to the release site. However, some lobsters at large 1−5 yr are still recaptured close to the release site (Krouse 1981; Campbell et al. 1984; Campbell and Stasko 1985). Single recapture methods supply a release and single recapture site, and it cannot be determined where or how far lobsters may have moved during extended periods between captures. Multiple recapture data in the present study provide two or more recapture sites for individual lobsters. Following an individual lobster movement over several months or years provides the opportunity of directly recording seasonal migration and homing tendencies.

## Methods

The paper examines movements of individual lobsters, recaptured several times over a period of 1−3 yr, with sufficient seasonal separation between recaptures to allow the geographical extremes of the migration to be detected. The data are drawn from a large tagging program (over 6285 lobsters tagged from May 1982 to November 1983) studying lobster growth and movements in the Browns Bank region of the Scotian Shelf (Fig. 1) (D. S. Pezzack and D. R. Duggan, unpubl. data).

Lobsters were caught in baited traps set between 100 and 500 m. Lobsters were measured, sexed, tagged with a sphyrion anchor tag (Scarratt and Elson 1965), and released within 5 min of capture. Offshore lobster fishermen recovered the majority of tagged lobsters recaptured. Offshore lobster fishing occurs year round, but fishing effort is highest between May and July (Pezzack and Duggan 1983). The fishery is concentrated to the southwest and southeast of Browns Bank, but is excluded from the Browns Bank lobster fishing closure area (Fig. 1). All recaptures within the closure area and intermediate recaptures of male lobsters were made during research cruises. Fishermen were paid a reward based on the amount of information accompanying each tag return (i.e. recapture location, depth, date, and carapace length (CL)). Fishermen were encouraged to record tag numbers, sex, and CL of all sublegal-sized and egg-bearing lobsters (illegal to land) and to return them to the sea with the tag still in place. All tagged lobsters caught during research cruises were recorded and released with the tag in place.

The distance moved by the lobster between captures was calculated from the straight-line distances between the two sites. The total distance moved was the sum of the straight-line distances between each recapture, and the net distance moved was the straight-line distance between the initial release and final recapture sites.

## Results

Of the 2486 lobsters recaptured between May 1982 and August 1985, 361 were recaptured more than once. Data from the majority of lobsters recaptured more than once were not useful for detecting round-trip migration and homing because they were either not at large long enough to complete a round-trip migration, intermediate recaptures were close together during the same season as initial release or final recapture, or the final recapture was during a different season than the release season. Only 8 of the 361 lobsters recaptured more then once had data useful in detecting annual movement away from the initial release site and a return movement. The eight lobsters used were at large 10−14 mo, the final recaptures were during the same season as released, the intermediate recaptures were in different seasons than the initial release.

Five of the eight lobsters analyzed made return movements. Two lobsters (Table 1; Fig. 1), lobsters 1 and 2, released during July 1982 and 1983, respectively, were recaptured in late summer of the year released, 110 and 152 km, respectively, from the initial release site. These lobsters were recaptured again in

TABLE 1. Summary of release and multiple recapture information for (a) eight lobsters at large 10–14 mo and recaptured in both summer–fall and winter–spring periods, (b) one lobster at large <10 mo and showing long-distance return movement, and (c) four lobsters at large >22 mo and showing long-distance return movement. Total distance is the sum of straight-line distances between subsequent recapture sites. Net distance is that between original release site and final recapture site. M = male; F = female.

| | Release | | | | Recapture | | | |
|---|---|---|---|---|---|---|---|---|
| Lobster | Carapace length (mm) | Sex | Date | Depth (m) | Months at large | Depth (m) | Total distance (km) | Net distance (km) |
| | | | *(a) At large 10–14 mo* | | | | | |
| 1 | 121 | F | July 14, 1982 | 113 | 2.5 | 168 | 110 | 110 |
| | | | | | 10.3 | 301 | 236 | 15 |
| | | | | | (40.2) | (119) | (248) | (3) |
| 2 | 115 | M | June 13, 1983 | 174 | 0.1 | 185 | 1 | 1 |
| | | | | | 2.4 | 128 | 152 | 152 |
| | | | | | 11.3 | 144 | 252 | 52 |
| | | | | | 12.6 | 168 | 298 | 12 |
| 3 | 133 | F | July 15, 1982 | 161 | 2.0 | 110 | 17 | 17 |
| | | | | | 3.0 | 110 | 27 | 25 |
| | | | | | 9.8 | 293 | 47 | 7 |
| 4 | 104 | F | July 14, 1982 | 113 | 1.3 | 124 | 13 | 13 |
| | | | | | 2.0 | 124 | 26 | 25 |
| | | | | | 11.3 | 110 | 68 | 19 |
| 5 | 117 | M | July 4, 1982 | 117 | 10.2 | 252 | 29 | 29 |
| | | | | | 14.2 | 124 | 69 | 13 |
| 6 | 143 | F | July 2, 1982 | 122 | 1.3 | 117 | 22 | 22 |
| | | | | | 10.2 | 311 | 168 | 163 |
| 7 | 111 | F | July 14, 1982 | 110 | 1.6 | 124 | 27 | 27 |
| | | | | | 12.1 | 168 | 163 | 111 |
| | | | | | 12.3 | 165 | 164 | 110 |
| 8 | 115 | M | May 31, 1983 | 267 | 1.7 | 110 | 15 | 15 |
| | | | | | 13.0 | 174 | 118 | 100 |
| | | | *(b) At large <10 mo* | | | | | |
| 9 | 136 | F | June 14, 1983 | 174 | 3.2 | 119 | 101 | 101 |
| | | | | | 5.9 | 172 | 211 | 9 |
| | | | *(c) At large >22 mo* | | | | | |
| 10 | 115 | F | May 29, 1983 | 282 | 3.8 | 168 | 128 | 128 |
| | | | | | 22.1 | 366 | 236 | 15 |
| 11 | 116 | F | May 27, 1983 | 302 | 2.4 | 168 | 125 | 125 |
| | | | | | 25.2 | 119 | 240 | 16 |
| 12 | 126 | F | July 3, 1982 | 115 | 17.5 | 170 | 114 | 114 |
| | | | | | 25.2 | 110 | 209 | 25 |
| 13 | 119 | F | July 26, 1982 | 122 | 2.1 | 188 | 121 | 121 |
| | | | | | 33.7 | 256 | 278 | 42 |

May and June of the next year 15 and 12 km, respectively, from their initial release site. The total distance moved was 236 and 298 km, respectively. Lobster 1 was released again and was recaptured 2.5 yr later within 3 km of the initial release site.

Three lobsters (lobsters 3, 4, and 5) travelled shorter total distances (47, 68, and 69 km, respectively) and showed return movements (lobsters 3 and 5) or reversal of direction (lobster 4), which could return it to the initial release site. The final recapture sites were 7, 19, and 13 km, respectively, from the initial release site (Table 1; Fig. 2). Three lobsters (lobsters 6, 7, and 8) showed no return movements (Table 1; Fig. 3).

The data on all lobsters recaptured more than once were examined to determine if any lobsters undertook return migrations in less than 10 or greater than 14 mo. One lobster (lobster 9), released in June 1983, completed a round-trip movement of 211 km in 6 mo (final recapture in December 1983), with a net movement of 15 km (Table 1; Fig. 1). Four lobsters (lobsters 10–13) were recaptured close to their initial release site (15, 16, 25, and 42 km, respectively) after 2 or 3 yr at large (22, 25, 25, and 34 mo) (Table 1; Fig. 4). The four lobsters had intermediate recapture sites over 114 km from the initial release sites.

## Discussion

Return migration and homing were observed in the majority of the eight lobsters for which sufficient data existed to allow detection of such movements. One lobster at large <10 mo and

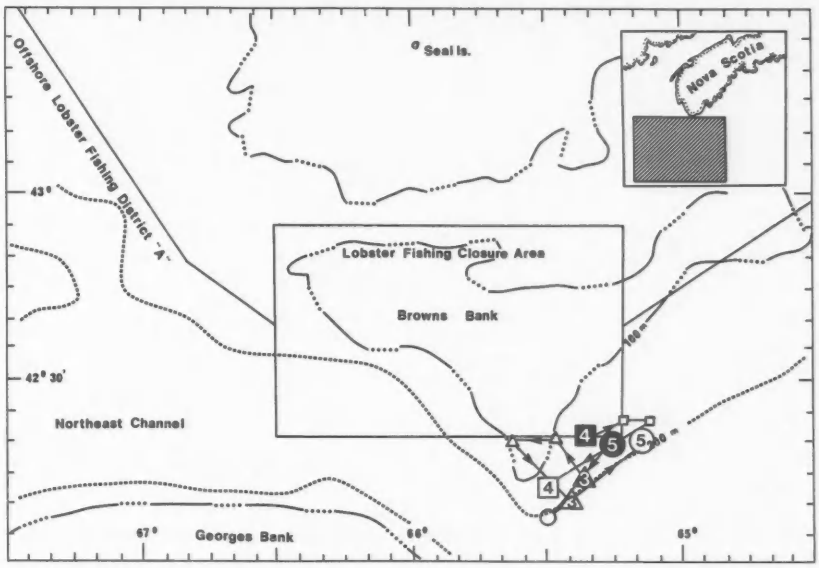


FIG. 2. Tagging locations (▲, ■, ●) and intermediate (△, □, ○) and final (△, □, ○) recapture sites of lobsters at large 10–14 mo (lobsters 3, 4, and 5) which undertook short-distance (<100 km) return movements (see Table 1 for dates and distances).

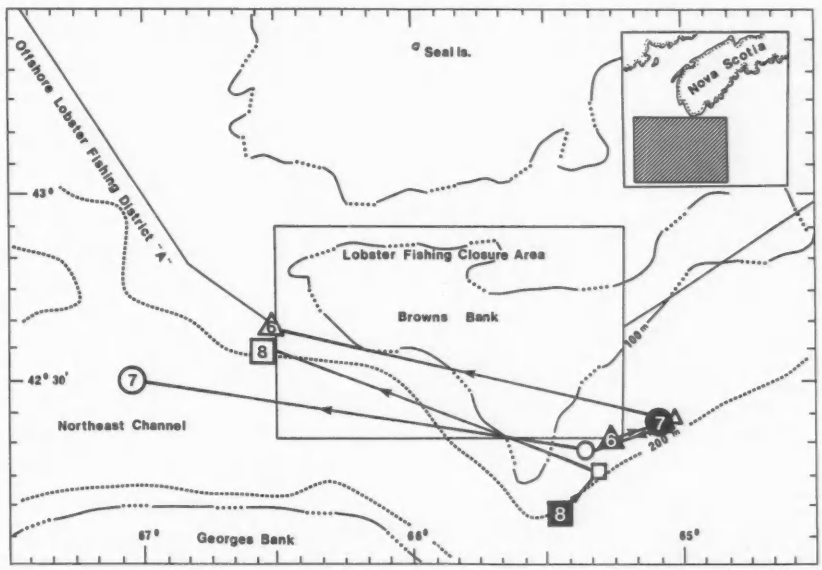


FIG. 3. Tagging locations (▲, ■, ●) and intermediate (△, □, ○) and final (△, □, ○) recapture sites of lobsters at large 10–14 mo (lobsters 6, 7, and 8) which did not show return movements (see Table 1 for dates and distances).

four at large >14 mo also showed homing tendencies.

Although caution must be exercised in interpretation of these data because the sample is small, this is the first direct evidence that long-distance return migrations and homing occur in lobsters.

Previous studies on lobster movements reported that a major portion of tag returns occurred close to the release area (Krouse 1980, 1981; Stasko 1980; Campbell 1982, 1984; Campbell et al. 1984; Campbell and Stasko 1985). The data presented in the present paper suggest that lobsters at large >10 mo and recaptured close to a release site could have migrated long distances and returned. Similarly, lobsters caught some distance from the release site during a different season than the release period might have returned to the original release area

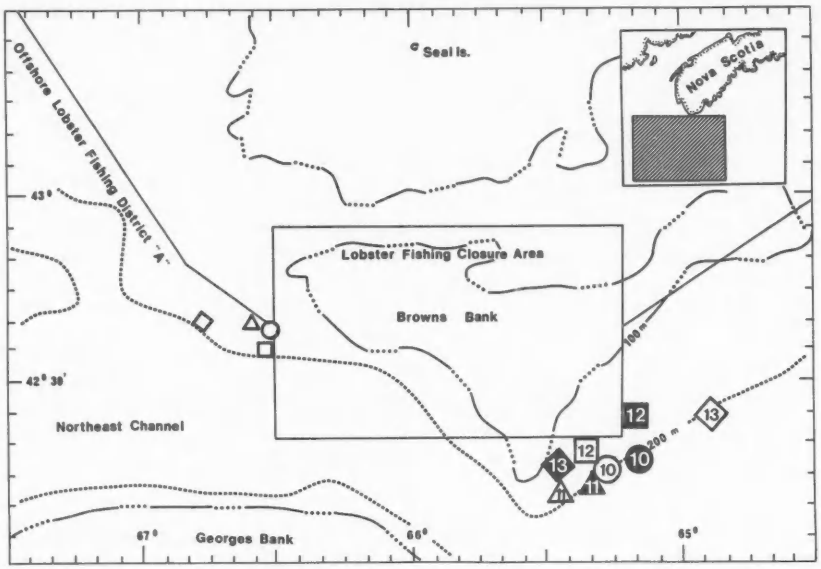


FIG. 4. Tagging locations (▲, ■, ●, ◆) and intermediate (△, □, ○, ◇) and final (△, □, ○, ◇) recapture sites of lobsters at large >22 mo (lobsters 10–13) which showed long-distance (>100 km) return movement (see Table 1 for dates and distances).

if they had remained at large. If long-distance return migrations are a general feature of lobster behavior, some of the conclusions of previous single recapture tagging data must be reevaluated.

The long-distance movements of mature lobsters observed in previous single recapture tagging studies (Uzmann et al. 1977; Campbell et al. 1984; Campbell and Stasko 1985) led to suggestions that there is extensive mixing of adult lobsters in the Gulf of Maine and that the entire Gulf might be considered a single population (Campbell and Mohn 1983; Campbell et al. 1984). Some of the observed long-distance movements may represent a portion of a round-trip migration. Permanent movement of lobsters out of a particular area may be small, and localized adult stocks could exist (i.e. Browns Bank region) if homing tendencies are strong. When interpreting tag return and fisheries data and developing management options for the lobster fishery, the possibility of homing and local adult stocks should be considered.

## Acknowledgements

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## References

CAMPBELL, A. 1982. Movements of tagged lobsters released off Port Maitland, Nova Scotia, 1944–80. Can. Tech. Rep. Fish. Aquat. Sci. 1136: 41 p.

1984. Aspects of lobster biology and fishery in the upper Bay of Fundy, p. 469–489. *In* D. C. Gordon Jr. and M. J. Dadswell [ed.] Update on the environmental consequences of tidal power development in the upper reaches of the Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1256: 469–489.

CAMPBELL, A., D. E. GRAHAM, H. J. MACNICHOL, AND A. M. WILLIAMSON. 1984. Movements of tagged lobsters released on the continental shelf from Georges Bank to Baccaro Bank, 1971–73. Can. Tech. Rep. Fish. Aquat. Sci. 1288: 16 p.

CAMPBELL, A., AND R. K. MOHN. 1983. Definition of American lobster stocks for the Canadian Maritimes by analysis of fishery-landing trends. Trans. Am. Fish. Soc. 112: 744–759.

CAMPBELL, A., AND A. B. STASKO. 1985. Movement of tagged American lobsters, *Homarus americanus*, off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 42: 229–238.

COOPER, R. A., AND J. R. UZMANN. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science (Wash., DC) 171: 288–290.

1980. Ecology of juvenile and adult *Homarus*, p. 97–142. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 2. Academic Press, New York, NY. 390 p.

DOW, R. L. 1974. American lobsters tagged by Maine commercial fishermen 1957–59. Fish. Bull. U.S. 72: 622–623.

ENNIS, G. P. 1984. Small-scale movements of the American lobster *Homarus americanus*. Trans. Am. Fish. Soc. 113: 336–338.

FOGARTY, M. J. D., D. V. D. BORDEN, AND H. J. RUSSEL. 1980. Movements of tagged American lobster, *Homarus americanus*, off Rhode Island. Fish. Bull. U.S. 78: 771–780.

HERRNKIND, W. F. 1980. Spiny lobster: patterns of movement, p. 349–407. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 1. Academic Press, New York, NY. 463 p.

KROUSE, J. S. 1980. Summary of lobster, *Homarus americanus*, tagging studies in American water (1889–1978). Can. Tech. Rep. Fish. Aquat. Sci. 932: 135–140.

1981. Movement, growth and mortality of American lobsters, *Homarus americanus*, tagged along the coast of Maine. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-747: 12 p.

MORRISSEY, T. D. 1971. Movements of tagged American lobsters, *Homarus americanus*, liberated off Cape Cod, Massachusetts. Trans. Am. Fish. Soc. 100: 117–120.

PEZZACK, D. S. 1984. Lobster distribution on the Scotian Shelf and implications to the Jonah crab fisheries. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 84/44: 17 p.

PEZZACK, D. S., AND D. R. DUGGAN. 1983. The Canadian offshore lobster (*Homarus americanus*) fishery — 1971 to 1982. Int. Counc. Explor. Sea Shellfish Comm. C.M.1983/K:34.

SAILA, S. B., AND J. M. FLOWERS. 1968. Movements and behavior of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. J. Cons. Int. Explor. Mer 31: 342–351.

SCARRATT, D. J., AND P. F. ELSON. 1965. Preliminary trials of a tag for salmon

and lobsters. J. Fish. Res. Board Can. 22: 421–423.

STASKO, A. B. 1980. Tagging and lobster movements in Canada. Can. Tech. Rep. Fish. Aquat. Sci. 932: 208–224.

STEEN, W. J. VAN DER. 1984. Methodological aspects of migration and orientation in fish, p. 421–444. *In* J. D. McCleave, G. P. Arnold, J. D. Dodson, and W. H. Neil [ed.] Mechanisms of migration in fish. Plenum Press, New York, NY. 500 p.

UZMANN, J. R., R. A. COOPER, AND K. J. PECCI. 1977. Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the southern New England continental shelf. NOAA Tech. Rep. NMFS SSRF-705: 92 p.

WILDER, D. G. 1963. Movements, growth and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. J. Fish. Res. Board Can. 20: 305–318.

# Recruitment of Packhorse Rock Lobster *Jasus verreauxi* in New Zealand

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Booth, J. D. 1986. Recruitment of packhorse rock lobster *Jasus verreauxi* in New Zealand.Can. J. Fish. Aquat. Sci. 43: 2212–2220.

The main breeding population of packhorse rock lobster *Jasus verreauxi* around mainland New Zealand is in the extreme north, near Cape Reinga. Some larvae from this area (and possibly some from Australia) are carried southeastward in the East Auckland Current along the east coast of North Island, and settlement occurs as far south as Cook Strait. Recapture of tagged animals shows that most juveniles migrate toward Cape Reinga where they mature and breed. The single major breeding population and migratory pathway may mean that the species is particularly vulnerable to overfishing. New Zealand and Australian stocks may be linked by larval transport across the north Tasman Sea.

La principale population de reproducteurs de la langouste *Jasus verreauxi* aux alentours des îles principales de la Nouvelle-Zélande se trouve à l'extrême nord, près du cap Reinga. Certaines larves provenant de ce secteur (et peut-être aussi d'Australie) sont transportées vers le sud-est par le courant East Auckland qui suit la côte est de l'île North, et elles viennent s'établir jusqu'au détroit de Cook. La recapture d'animaux marqués montre que la plupart des juvéniles migrent en direction du cap Reinga, où ils atteignent la maturité sexuelle et se reproduisent. L'existence d'une seule grande population de reproducteurs et d'une seule voie migratoire peut signifier que l'espèce est particulièrement vulnérable à la surpêche. Les stocks de Nouvelle-Zélande et d'Australie peuvent être liés par le transport de larves dans la partie nord de la mer de Tasman.

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The packhorse or green rock lobster *Jasus verreauxi* (H. Milne Edwards) (Decapoda: Palinuridae) occurs in New Zealand, where it is fished mainly in the north (Booth 1979), and also in Australia (George 1966). Together with the much more abundant and widespread red rock lobster *J. edwardsii*, it forms a valuable inshore New Zealand fishery. An understanding of recruitment in both species is needed to manage this resource.

Large quantities of packhorse were taken along the east coast of North Island as far south as eastern Bay of Plenty during early years of the fishery (Kensler and Skrzynski 1970). In 1969, the minimum legal size (MLS) was increased from a 6-in. (152-mm) tail length to 8.5 in. (216 mm) (equivalent to about 163 mm antennal carapace length (CL) for males and 155 mm CL for females) (Booth 1979). The fishery became centred near Cape Reinga (Fig. 1) where most large animals were available.

Size at onset of breeding of packhorse females (the smallest size at which at least 50% bear eggs) is at least 160 mm CL, generally more than 10 mm CL (and 2 yr of growth) greater than the size at which setae first develop on the endopodites of the pleopods (Kensler 1967a; Booth 1984a). The only known large population of breeding females is west of North Cape, near Cape Reinga. They occur in much smaller numbers to the south, seldom south of Whangarei Heads on the east coast, but occasionally to Foveaux Strait on the west coast (Booth 1979, 1984a, unpubl.).

Most mature female packhorse breed once a year. They become egg-bearing in shallow (<60 m), inshore areas in October. Hatching to naupliosoma larvae occurs at greater depths (≥100 m), principally during December and January (Kensler 1967b; Lesser 1974; Booth 1984a, unpubl.). The phyllosoma larva (plural phyllosomas according to Webster's Third New International Dictionary of the English Language, 1981) is a flat, transparent larva typical of spiny (rock) lobsters and occurs after the naupliosoma stage. Phyllosomas are transported by currents, although their diurnal movements in the water column may result in less horizontal transport than would be expected from generally recognised current patterns.

In several rock lobster species, late-stage phyllosomas occur exclusively beyond the edge of the continental shelf, and the animals return to the shore after metamorphosis to the puerulus stage. Pueruli (from L. puerulus n., plural pueruli) are transitional between phyllosomas and juveniles, resemble adults in shape, and are capable of directional swimming.

This paper investigates the role in *J. verreauxi* recruitment of the distribution of breeding females, water flow patterns, settlement patterns, and movements by juveniles. Also, the relationship between New Zealand and Australian stocks is discussed.

## Distribution of Packhorse around New Zealand

Packhorse have been reported commonly from around

FIG. 1. Mainland New Zealand showing localities mentioned in text. Kermadec Islands are 980 km northeast of East Cape; Chatham Islands are 810 km east of Banks Peninsula.

mainland New Zealand, and rarely from Kermadec and Chatham Islands (Chilton 1911; Kensler 1967c; Booth and Saxton 1983). Although present distribution patterns appear to be similar to those for earlier years of the fishery described by Kensler and Skrzynski (1970), additional and more detailed information on the distribution of particular size groups of packhorse is now available. This information has come from catch sampling observations (Booth 1979, 1984a, 1984b, unpubl.), from Marine Department (later Ministry of Agriculture and Fisheries) commercial fish landing statistics (e.g. Sanders 1984), and from commercial pot fishermen and amateur divers.

The abundance and size of packhorse vary considerably around New Zealand (Fig. 2). The species is caught most commonly along the north and east coasts of North Island north of Cape Turnagain. They are rare along the east coast of South Island and in Foveaux Strait, but are occasionally taken along the entire west coast of the country and also through Cook Strait. The species has not been reported from Stewart Island, Snares Islands, nor from any of New Zealand's subantarctic islands despite intensive potting in some of these areas.

Packhorse less than MLS predominate along the east coast of North Island. These animals occur at depths of 20–130 m,

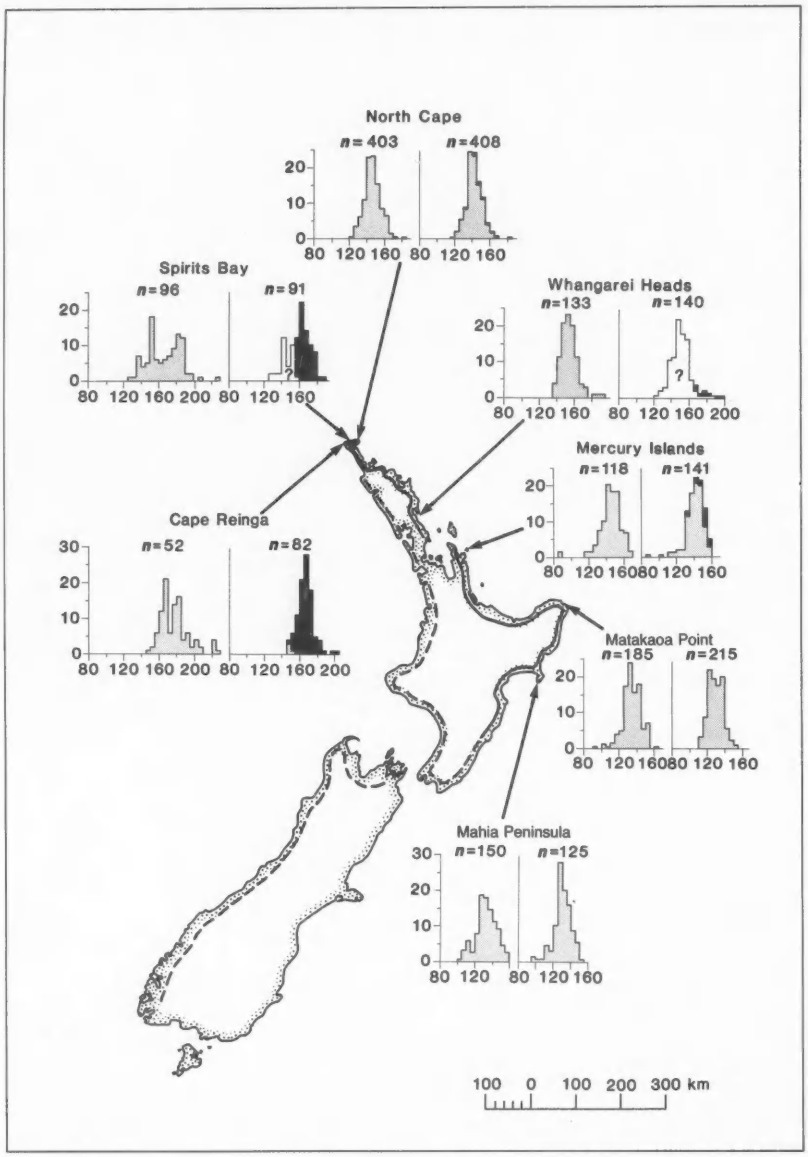


FIG. 2. Distribution of *Jasus verreauxi* around mainland New Zealand. On the map, continuous line is area of major occurrence; broken line is area of occasional occurrence. Histograms give carapace length–frequency distributions from pot catches (Booth 1979, 1984b, unpubl.; Booth and Bycroft 1982) for males (left) and females (right). Black, females with setae; ?, unknown.

often to the south of headlands which extend into the generally south-flowing coastal current. Not only does the proportion of undersized specimens in pot catches along the east coast of North Island increase with distance south, at least as far as Mahia Peninsula, but there is also evidence for a decrease in mean size of the undersized rock lobsters (Fig. 2). Although specimens <100 mm CL occur along the entire east coast of North Island, most diver reports of specimens <40 mm CL have been from near East Cape. The high numbers of small rock lobsters off North Cape, together with their movements, led in 1977 to a ban on commercial rock lobster fishing (Booth 1979). The mean size of packhorse off North Cape, 4.5 yr after the ban was imposed, was the same as that during the period of moderate to high fishing pressure in the mid-1960s (Booth and Bycroft 1982; Booth, unpubl.). Apparently, fishing pressure has not been the main cause of the high proportion of undersized animals present there.

The most important commercial fishery in the country is located within a 25-km radius of Cape Reinga in depths of 50–150 m, although packhorse greater than MLS occur com-

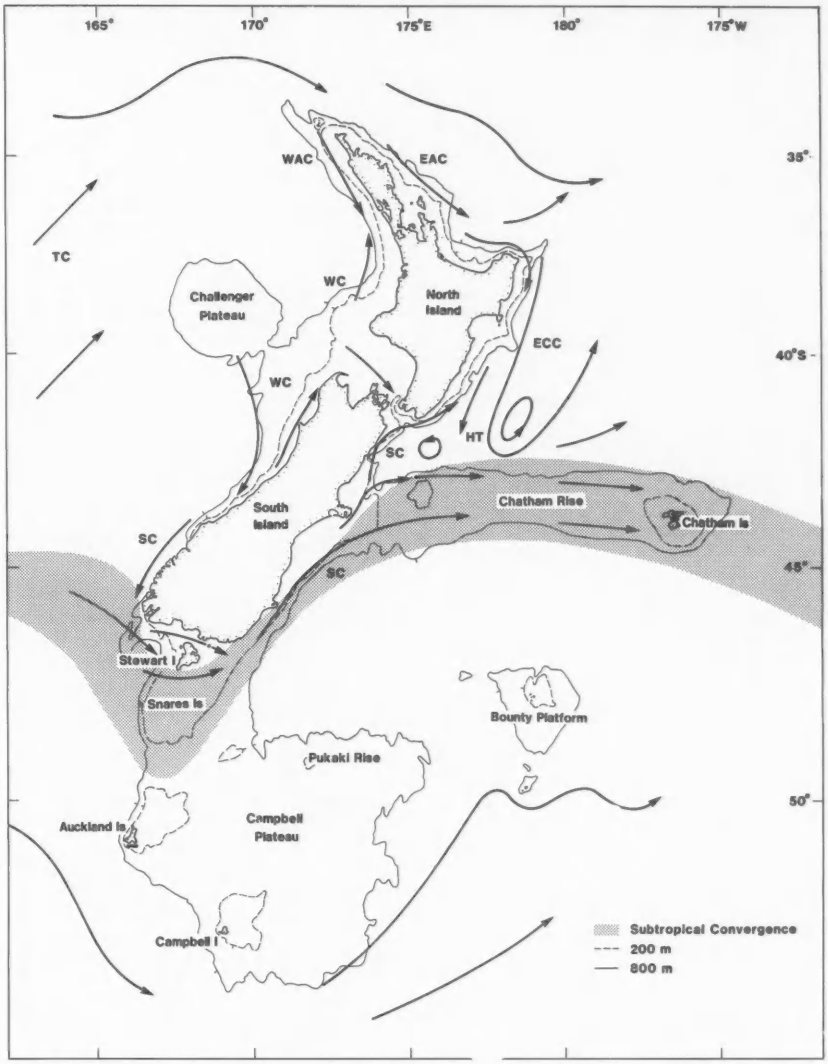


FIG. 3. New Zealand region showing major surface currents and other oceanographic features. Bathymetry in metres. EAC, East Auckland Current; ECC, East Cape Current; HT, Hikurangi Trough; SC, Southland Current; TC, Tasman Current; WAC, West Auckland Current; WC, Westland Current.

monly along the east coast north of Mercury Islands. Legal-sized specimens have also occurred in pot catches from Wanganella Bank, about 530 km northwest of Cape Reinga (E. B. Green, Fisheries Management Division, MAF, Private Bag, Auckland, pers. comm.). Large specimens (≥180 mm CL) are seldom taken south of Whangarei Heads on the east coast, but most from the west coast of South Island south of Jackson Head are large.

The most obvious change in packhorse sizes since the 1960s has been the reduction in proportion of legal-sized and mature specimens taken from east coast areas south of North Cape (e.g. Bay of Plenty). In contrast, a high proportion of large packhorse has been available throughout the development of the Cape Reinga fishery (Kensler and Skrzynski 1970; Booth 1979, 1984a).

## Occurrence of Larval and Early Juvenile Packhorse in Relation to Water Flow

### Oceanic Water Flow around New Zealand

Oceanic flow patterns affect the distribution of palinurid larval stages. The general flow past New Zealand is from west to east (Fig. 3). The Tasman Current along the west coast of the country is a generally slow, northeastward flow of Subtropical Water derived from the East Australian Current (Stanton 1973a). Nearshore parts of Northland are influenced by two currents. Sometimes present along the west coast is the West Auckland Current (WAC), a weak, surface, south-flowing coastal current of Subtropical Water that extends at least 100 km offshore (Garner 1961; Ridgway 1980). Its southern

TABLE 1. Numbers and sizes of *Jasus verreauxi* tagged around North Island, 1976–82, and numbers and sizes of those recaptured ≥15 km from tagging site by 31 May 1985. For details of tagging locations, see Booth (1979, 1984b). CL, antennal carapace length; M, male; F, female.

| | No. tagged | | Sizes (mm CL) at tagging | | Recaptures by 31 May 1985 | | Size range (mm CL) of recaptures | |
|---|---|---|---|---|---|---|---|---|
| Tagging locations and years | M | F | M | F | M | F | M | F |
| North Cape, 1976–78 | 476 | 538 | 106–172 | 111–174 | 60 | 79 | 132–187 | 129–189 |
| Whangarei Heads, 1979–80 | 133 | 140 | 135–195 | 121–196 | 10 | 4 | 145–174 | 150–166 |
| Mercury Islands, 1979–82 | 122 | 150 | 87–166 | 89–157 | 7 | 4 | 124–167 | 153–168 |
| Matakaoa Point, 1981 | 185 | 215 | 91–162 | 111–150 | 2 | 8 | 143–154 | 146–165 |
| Gisborne, 1979–81 | 23 | 16 | 98–138 | 81–130 | 1 | 1 | 134 | 143 |
| Mahia Peninsula, 1978–82 | 150 | 125 | 100–158 | 98–151 | 9 | 8 | 132–157 | 123–145 |
| Total | 1089 | 1184 | | | 89 (8.2%) | 104 (8.8%) | | |

limit is variable, but is most frequently in the Kaipara Harbour–Waikato River region. The East Auckland Current (EAC) is a small, persistent, western boundary current of subtropical origin (Brodie 1960) flowing towards East Cape. Flowing south of East Cape, on the western side of Hikurangi Trough, is the inshore arm of the East Cape Current (ECC) (Fleming 1950). Near the head of Hikurangi Trough (41°S, 178°E), this arm meets the northward flow of the Southland Current, and its direction is reversed mainly because of constraints of the bottom topography. Part of the flow does not join the eddy thus formed, but moves northeastward along the eastern side of Hikurangi Trough, forming the outer arm of the ECC. The rest meanders generally eastward to contribute to the Subtropical Convergence. South of Cook Strait, the flow is generally from the south.

A few large, permanent eddy-like features have been identified off the north and east coasts of North Island. Sampling of temperature and salinity and the release of drift cards and buoys during 1977–80 provided no evidence for them within 30 km of the Northland coastline between Tauroa Point and Cape Karikari (Booth, unpubl.). However, further off the coast between North Cape and Cape Turnagain, some eddy-like structures have been observed (Barker and Kibblewhite 1965; Garner 1969a; Ridgway 1970; Bradford et al. 1982; Denham et al. 1984). Probably the most prominent recirculation occurs within the anticyclonic eddy centred near the head of Hikurangi Trough, at the southern end of the ECC system. Some recirculation within the EEC system as a whole may also occur (as suggested by fig. 6 in Heath 1975).

### Occurrence of Phyllosoma and Early Juvenile Stages around New Zealand

All packhorse phyllosomas (8) and pueruli (13) taken around New Zealand came from eastern areas of North Island as far south as Castlepoint. (Identifications were based on Lesser (1974), McWilliam and Phillips (1986), and Archey (1916). Details of these collections can be obtained from the author.) This is the same region in which juveniles are most commonly caught. These distributions are consistent with the generally recognised oceanic flow patterns around North Island, assuming that packhorse phyllosomas exercise little or no control over their general direction of alongshore transport. A larval life of 8–12 mo for *J. verreauxi* is possible, based on the capture during spring and summer of most of the late-stage phyllosomas, as well as pueruli and early post-pueruli. A similar length of larval stage is observed for *J. verreauxi* in Australia (C. Lee, Thai-Australian Tung Kula Ronghai Project, P.O. Box 100, Amphur Muang, Roi-Et 45000, Thailand, pers. comm.). However, with such small numbers of specimens this estimate must be considered provisional.

Although the east coast of North Island has been sampled most intensively for phyllosomas and pueruli, unproductive effort expended elsewhere around New Zealand (Booth 1983a, 1984c, unpubl.; Booth and Tarring 1982) indicates that this is probably not the principal reason most packhorse specimens have been caught in the east. The plankton sampling included an investigation into the occurrence of mid- and late-stage packhorse phyllosomas, as well as pueruli, near the Cape Reinga breeding grounds (Booth, unpubl.). Stations within the shelf edge between Tauroa Point and Cape Karikari were sampled at night about every 3 mo, using various-sized nets with 7-mm mesh, from March 1977 to January 1978 and again in August and November 1978. Although similar sampling strategies used beyond the shelf edge elsewhere resulted in the capture of palinurid and scyllarid phyllosomas and pueruli, only scyllarids were taken during 1977–78, indicating little packhorse phyllosoma development in waters within the shelf edge in the north of the country.

## Alongshore Movements of Juvenile Packhorse

A total of 2273 packhorse (81–196 mm CL) were tagged at six localities along the north and east coasts of North Island during 1976–82 (Table 1). Most females were immature; males were of similar size, but their maturity was not determined. Some rock lobsters were recaptured locally (<15 km from tagging site), while others of both sexes made long-distance (≥15 km) movements. The long-distance movements through 31 May 1985 shown in Fig. 4 include those ≥15 km previously reported by Booth (1979, 1984b). Most (99.0%) movements were generally northwestward against the prevailing coastal current towards the breeding area off Cape Reinga, and there was no evidence for any return movements. Because areas further to the north and west of Cape Reinga are not regularly fished, it is not known if any packhorse continued to move in these directions. The available data point to the Cape Reinga area being the ultimate destination. However, a few animals (4.2%) moved southward along the west coast, and, at least in the central part, this movement was also against the coastal current.

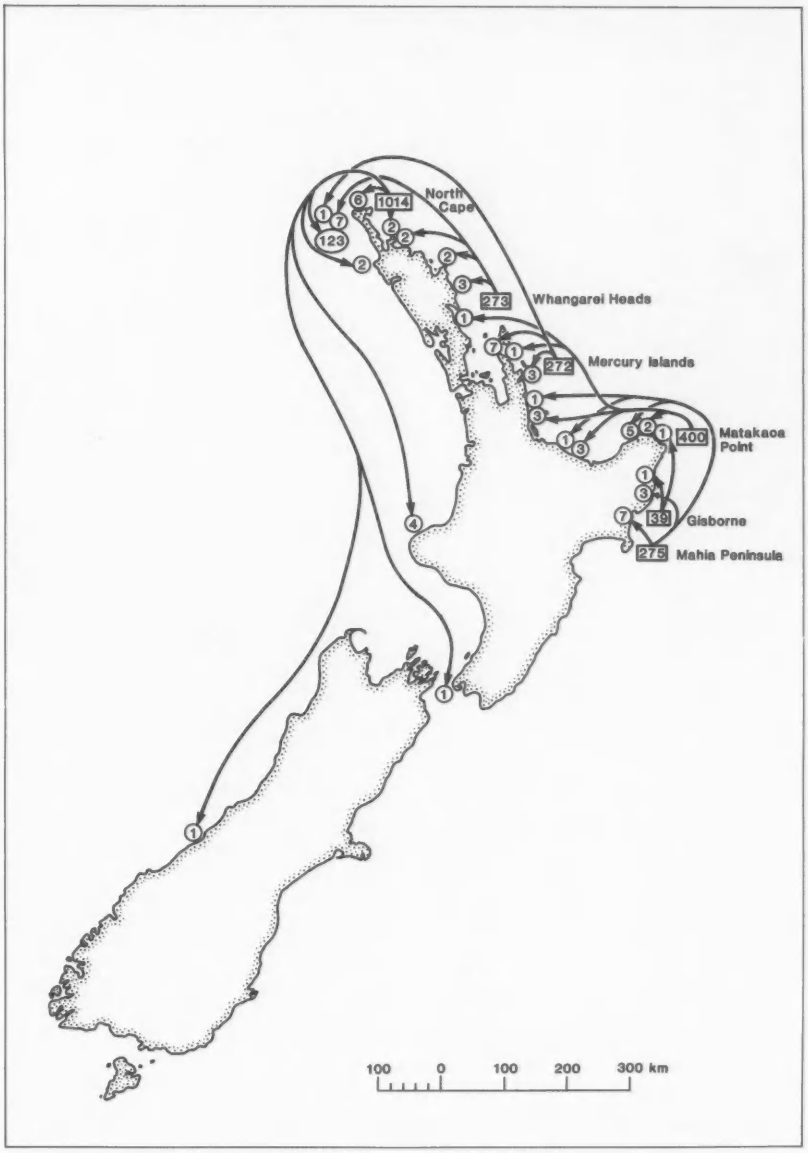


FIG. 4. Long-distance (≥15 km) movements of *Jasus verreauxi* tagged at six locations around North Island during 1976–82 and recaptured by 31 May 1985. Number in box gives number of animals tagged; line gives inferred movement; encircled number gives number of tagged rock lobsters recaptured at or near that point. For other details, see Table 1.

Long-distance movements by lobsters of at least 200 km occurred from all tagging sites (Table 2). With the exception of that for Mercury Islands (where several packhorse were caught soon after tagging), the smallest mean, straight-line distance moved from any tagging site (86 km) was from North Cape, the site closest to the main breeding area off Cape Reinga. The greatest distance covered by any individual was 1070 km, at a rate of 0.63 km·d$^{-1}$. Other rates of movement ranged between 0.03 and 3.36 km·d$^{-1}$. It seems likely from distributional and tag return data that most of the mainly large packhorse occurring along the west and south coasts of New Zealand arrived there by migration from the north, rather than from local pueruli settlement. Animals occurring in Foveaux Strait probably migrated there via Cape Reinga after settlement along the east coast of North Island, a straight-line migration of 1400–2400 km.

The size at which rock lobsters begin to move long distances is unclear. Few animals <100 mm CL have been tagged, but no animals <120 mm CL at recapture had moved long distances. The majority of those which moved long distances were

TABLE 2. Distances and rates of movement of *Jasus verreauxi* tagged around North Island, 1976–82, and recovered ≥15 km from tagging site by 31 May 1985.

| Location | No. recaptured | Distance moved (km) | | Rate ($km \cdot d^{-1}$) | |
|---|---|---|---|---|---|
| | | Mean | Range | Mean | Range |
| North Cape | 139 | 86 | 21–1070 | 0.31 | 0.03–3.36 |
| Whangarei Heads | 14 | 189 | 19–322 | 0.77 | 0.15–1.70 |
| Mercury Islands | 11 | 75 | 15–401 | 0.39 | 0.04–1.69 |
| Matakaoa Point | 10 | 187 | 32–384 | 0.50 | 0.13–1.05 |
| Gisborne | 2 | 145 | 80–209 | 0.26 | 0.10–0.42 |
| Mahia Peninsula | 17 | 138 | 44–417 | 0.59 | 0.14–1.73 |

125–160 mm CL at tagging and 135–175 mm CL at recapture. Most female packhorse (93%) lacked setae when tagged, but the majority (86%) of those recaptured west of North Cape and along the west coast of New Zealand had setae. Most animals of both sexes recaptured in these areas had reached legal size and had changed colour from the dark green of juveniles to the olive green of adults. None of the few large, mature animals tagged moved significantly.

## Discussion

### Packhorse Breeding near Cape Reinga

The high proportion of mature and egg-bearing packhorse in the more northern parts of New Zealand is not necessarily due only to the warm sea temperatures there. Water temperatures throughout the water column near the 100-m isobath around northern New Zealand between Cape Egmont and East Cape vary little with locality during both summer and winter (Garner 1969b). Historically, large numbers of breeding animals occurred to the south (e.g. Bay of Plenty) and they are still occasionally taken there. Therefore, other factors probably are important in Cape Reinga being the major breeding area for *J. verreauxi*. This region is well known for upwellings and strong tidal currents (Stanton 1973b). *Jasus lalandii* releases larvae at times of upwelling on the west coast of South Africa, thereby facilitating not only dispersal, but also ensuring food for the larvae (George et al. 1970, cited in Phillips 1981). Ovigerous *J. edwardsii* sometimes accumulate in areas of strong water movement (McKoy and Leachman 1982), presumably to ensure greater larval dispersal and reduced predation. At Cape Reinga, therefore, all three factors — high sea temperature and the upwelling and strong currents nearby — may be important to successful breeding of *J. verreauxi*.

### Distribution of Phyllosoma Larvae

Although early-stage packhorse phyllosomas may initially be carried southward along the west coast of Northland by the WAC, plankton sampling has pointed to few remaining in the inshore areas of Northland to reach mid- or late stage. The occurrence of early juvenile stages onshore indicates that some larvae are carried around northern New Zealand to occur in the EAC and ECC, and probably in waters beyond those flows. The small numbers of *J. verreauxi* reported from Kermadec and Chatham Islands may result from generally eastward larval drift from mainland New Zealand. However, it seems likely that many of the larvae carried much beyond these flows will tend to be lost from New Zealand.

The relatively fast flow rates in the EAC and the inner arm of the ECC ($0.1–0.3\ m \cdot s^{-1}$) (Heath 1975, 1980), together with the several months' larval stage, suggest that oceanographic and/or biological factors help to retain some larvae nearshore in the generally east-directed flow past New Zealand. Nearshore currents may be more complex and variable than presently recognised, resulting in reduced net larval drift. Eddies and meanders, particularly those off the east coast of North Island between East Cape and Cook Strait, may keep larvae nearshore. The ECC system itself is possibly crucial in this, as the occurrence of early stages of *J. verreauxi* in this area, in addition to high catches of *J. edwardsii* phyllosomas and pueruli (Booth 1984c, unpubl.) suggest. Furthermore, larvae may be able to control their direction of transport by varying the length of time they spend at particular depths. It may therefore be possible for larvae to be carried well offshore but to be returned within a subsurface drift not presently recognized.

### Movements of Juvenile Packhorse

Assuming little or no larval recruitment from outside New Zealand, the known current patterns and length of the larval stage are such that, unless some rock lobsters migrate against the water flow, the species could be continually displaced to the south and east. Other palinurids in which there are migrations in a direction opposite to the prevailing current include *J. edwardsii* in southern New Zealand (Street 1973) and *Panulirus ornatus* in Torres Strait (Moore and MacFarlane 1984). The movement of female packhorse while immature is in keeping with several other palinurids, including *J. edwardsii* in southern New Zealand and *Panulirus cygnus* off Western Australia (Street 1973; George 1958). Some juvenile *J. edwardsii* along the east coast of North Island may move northwards in a similar manner to packhorse; some evidence for this has come from tagging studies near Gisborne (Booth, unpubl.).

It appears that most packhorse along the east coast of North Island eventually move northward. Large ones primarily occur west of North Cape, and few greater than MLS are caught south of Mercury Islands. Either the rock lobsters move out of those areas or they become unavailable to potting for other reasons. Since most packhorse seem to migrate along a single pathway to reach one major breeding area, the species may be particularly vulnerable to overfishing.

### Possible Relationship with Australian Stocks of *J. verreauxi*

Williamson (1967) took the presence of non breeding *J. verreauxi* along the west coast of North Island as evidence for drift of packhorse larvae from Australia to New Zealand. Although their presence is accounted for by the movement patterns reported here, some larval recruitment from Australia remains a possibility. An east-directed flow of water around

34°S from the east coast of Australia links at least part of the East Australian Current to the flow off the east coast of New Zealand, the other western boundary current in the subtropical gyre.

Breeding *J. verreauxi* mainly occur along the east coast of Australia north of about 33°S, with juveniles to the south (Williamson 1967; R. J. MacIntyre, University of New South Wales, Kensington, Sydney, New South Wales, pers. comm.). Some larvae are probably carried southward in the East Australian Current to New South Wales and occasionally even to southern Tasmania (Hickman 1946). There may then be contranatant movements by some juveniles, similar to those in New Zealand, toward breeding areas in the north. However, other larvae could in some years be transported the 1900 km to New Zealand (or further, to Kermadec Islands) on the eastward flow at 34°S. The scarcity of young packhorse along the west coast of South Island makes it less likely that phyllosomas are transported in the more southerly flow towards New Zealand described by Stanton (1973a). Transit times at 34°S would vary because of meanders and eddies (Stanton 1981) but, according to Wyrtki's (1960) observations, could be as short as 3–4 mo. Bradford (1977) concluded that this eastward flow transported the pelagic copepod *Temora turbinata* to New Zealand. Similarly, long-distance transport of *Jasus tristani* larvae in the South Atlantic Ocean has been proposed (Lutjeharms and Heydorn 1981). However, the evolution in New Zealand of a strong contranatant migration of packhorse suggests that most larvae originate from local hatching.

Some packhorse (and *J. edwardsii*) larvae from New Zealand could be carried towards the east Australian coast. Hatching of *J. verreauxi* eggs occurs off northern New Zealand during summer, when the westward-flowing Trade Wind Drift field and the Tropical Convergence are furthest south (Stanton 1975). At this time some water along the west coast of Northland may, under the influence of the prevailing easterly winds, flow north and then west, rather than eastward around the north of the country (e.g. Garner 1959). Various observations (Dell 1952; Wyrtki 1960; Cresswell 1976; Quincey 1977; Booth 1983b) support the presence at times of westward drift across almost the entire north Tasman Sea.

### Summary of Recruitment of *J. verreauxi*

It is proposed that the main breeding population of *J. verreauxi* in New Zealand is in the extreme north, near Cape Reinga. Eggs hatch during summer, and, although many phyllosomas initially may be carried southward by the WAC, most are transported offshore. Some larvae may be lost to the north and west, while others are carried eastward and then southeastward in the EAC and ECC. It is possible that some packhorse larvae from Australia also contribute to this larval stock. Some late-stage phyllosomas metamorphose and settle as pueruli along the east coast of North Island. Others may be carried eastward to colonize Kermadec and Chatham Islands, or to be lost from New Zealand. Most late juveniles along the east coast of North Island migrate northwards toward the breeding area off Cape Reinga, while a few move southward along the west coast of New Zealand. Females reaching the Cape Reinga area will not breed for at least 2 yr.

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## References

ARCHEY, G. 1916. Notes on the marine crayfish of New Zealand. Trans. Proc. N.Z. Inst. 48: 396–406.

BARKER, P. H., AND A. C. KIBBLEWHITE. 1965. Physical oceanographic data from the Tui cruise, 1962. N.Z. J. Sci. 8: 604–634.

BOOTH, J. D. 1979. North Cape — a 'nursery area' for the packhorse rock lobster, *Jasus verreauxi* (Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 13: 521–528.

1983a. Power station attracts rock lobster larvae. Catch 10(5): 15.

1983b. Getting the drift of lobster larvae. Catch 10(8): 12.

1984a. Size at onset of breeding in female *Jasus verreauxi* (Decapoda: Palinuridae) in New Zealand. N.Z. J. Mar. Freshwater Res. 18: 159–169.

1984b. Movements of packhorse rock lobsters (*Jasus verreauxi*) tagged along the eastern coast of the North Island, New Zealand. N.Z. J. Mar. Freshwater Res. 18: 275–281.

1984c. Rock lobster fishery causes concern. Catch 11(2): 12, 21–23.

BOOTH, J., AND B. BYCROFT. 1982. Little change in lobsters at North Cape. Catch 9(2): 28.

BOOTH, J., AND F. SAXTON. 1983. Packhorse capture "a first". Catch 10(5): 29.

BOOTH, J., AND S. TARRING. 1982. Settlement of larval rock lobsters. Catch 9(6): 10–14.

BRADFORD, J. M. 1977. Distribution of the pelagic copepod *Temora turbinata* in New Zealand coastal waters, and possible trans-Tasman population continuity. N.Z. J. Mar. Freshwater Res. 11: 131–144.

BRADFORD, J. M., R. A. HEATH, F. H. CHANG., AND C. H. HAY. 1982. The effect of warm-core eddies on oceanic productivity off north-eastern New Zealand. Deep-Sea Res. 29: 1501–1516.

BRODIE, J. W. 1960. Coastal surface currents around New Zealand. N.Z. J. Geol. Geophys. 3: 235–252.

CHILTON, C. 1911. The Crustacea of the Kermadec Islands. Trans. N.Z. Inst. 43: 544–573.

CRESSWELL, G. R. 1976. A drifting buoy tracked by satellite in the Tasman Sea. Aust. J. Mar. Freshwater Res. 27: 251–262.

DELL, R. K. 1952. Ocean currents affecting New Zealand. N.Z. J. Sci. Technol. Sect. B 34: 86–91.

DENHAM, R. N., R. W. BANNISTER, K. M. GUTHRIE, AND F. G. CROOK. 1984. Surveys of the East Auckland and East Cape Currents, New Zealand. Aust. J. Mar. Freshwater Res. 35: 491–504.

FLEMING, C. A. 1950. Some South Pacific sea-bird logs. Emu 49: 169–188.

GARNER, D. M. 1959. The Sub-tropical Convergence in New Zealand surface waters. N.Z. J. Geol. Geophys. 2: 315–337.

1961. Hydrology of New Zealand coastal waters, 1955. N.Z. Oceanogr. Inst. Mem. 8: 85 p.

1969a. The geopotential topography of the ocean surface around New Zealand. N.Z. J. Mar. Freshwater Res. 3: 209–219.

1969b. The seasonal range of sea temperature on the New Zealand shelf. N.Z. J. Mar. Freshwater Res. 3: 201–208.

GEORGE, R. W. 1958. The status of the "white" crayfish in Western Australia. Aust. J. Mar. Freshwater Res. 9: 537–545.

1966. Marine crayfish or spiny lobsters of Australia. Aust. Fish. Newsl. 25(5): 25–28.

HEATH, R. A. 1975. Oceanic circulation off the east coast of New Zealand. N.Z. Oceanogr. Inst. Mem. 55: 80 p.

1980. Eastwards oceanic flow past northern New Zealand. N.Z. J. Mar. Freshwater Res. 14: 169–182.

HICKMAN, V. V. 1946. Notes on the Tasmanian marine crayfish, *Jasus lalandii* (Milne Edwards). Pap. Proc. R. Soc. Tasmania 1945: 27–38.

KENSLER, C. B. 1967a. Size at first maturity in females of the spiny lobster *Jasus verreauxi* (Crustacea: Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 1: 327–340.

1967b. Fecundity in the marine spiny lobster *Jasus verreauxi* (H. Milne Edwards) (Crustacea: Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 1: 143–155.

1967c. The distribution of spiny lobsters in New Zealand waters (Crustacea: Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 1: 412–420.

KENSLER, C. B., AND W. SKRZYNSKI. 1970. Commercial landings of the spiny lobster *Jasus verreauxi* in New Zealand (Crustacea: Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 4: 46–54.

LESSER, J. H. R. 1974. Identification of early larvae of New Zealand spiny and shovel-nosed lobsters (Decapoda, Palinuridae and Scyllaridae). Crustaceana (Leiden) 27: 259–277.

LUTJEHARMS, J. R. E., AND A. E. F. HEYDORN. 1981. The rock-lobster *Jasus tristani* on Vema Seamount: drifting buoys suggest a possible recruiting mechanism. Deep-Sea Res. 28A: 631–636.

MCKOY, J. L., AND A. LEACHMAN. 1982. Aggregation of ovigerous female rock lobsters, *Jasus edwardsii* (Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 16: 141–146.

MCWILLIAM, P. S., AND B. F. PHILLIPS. 1986. Distinguishing the phyllosoma larvae of rock lobster species of the genus *Jasus* (Decapoda: Palinuridae) in the waters of Australia and New Zealand. Crustaceana (Leiden). (In press)

MOORE, R., AND J. W. MACFARLANE. 1984. Migration of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua New Guinea. Aust. J. Mar. Freshwater Res. 35: 197–212.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

QUINCEY, C. 1977. Tasman trespasser. Hodder & Stoughton, Auckland. 203 p.

RIDGWAY, N. M. 1970. Hydrology of the southern Kermadec Trench region. N.Z. Oceanogr. Inst. Mem. 56: 30 p.

1980. Hydrological conditions and circulation off the west coast of the North Island, New Zealand. N.Z. J. Mar Freshwater Res. 14: 155–167.

SANDERS, B. M. 1984. The 1983 New Zealand rock lobster landings. Fish. Res. Div. Occas. Publ. Data Ser. (N.Z.) 16: 31 p.

STANTON, B. R. 1973a. Circulation along the eastern boundary of the Tasman Sea, p. 141–147. *In* R. Fraser [comp.] Oceanography of the South Pacific 1972. N.Z. National Commission for UNESCO, Wellington.

1973b. Hydrological investigations around northern New Zealand. N.Z. J. Mar. Freshwater Res. 7: 85–110.

1975. Vertical structure in the mid-Tasman convergence zone. N.Z. J. Mar. Freshwater Res. 9: 63–74.

1981. An oceanographic survey of the Tasman Front. N.Z. J. Mar. Freshwater Res. 15: 289–297.

STREET, R. J. 1973. Trends in the rock lobster fishery in southern New Zealand 1970–71. N.Z. Minist. Agric. Fish. Fish. Tech. Rep. 116:13 p.

WILLIAMSON, D. I. 1967. Some recent advances and outstanding problems in the study of larval crustacea, p. 815–823. *In* Proceedings of the Symposium on Crustacea — Part II. Marine Biological Society of India.

WYRTKI, K. 1960. The surface circulation in the Coral and Tasman Seas. CSIRO Div. Fish. Oceanogr. Tech. Pap. 8: 44 p.

# Settlement of Spiny Lobster, *Panulirus argus*, Pueruli in South Florida: An Evaluation from Two Perspectives

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Marx, J. M. 1986. Settlement of spiny lobster, *Panulirus argus*, pueruli in south Florida: an evaluation from two perspectives. Can. J. Fish. Aquat. Sci. 43: 2221–2227.

Settlement of spiny lobster, *Panulirus argus*, pueruli occurs year-round in south Florida, but seasonal trends are not consistent. Recruitment peaks are common in spring but sometimes occur in other seasons. Postsettlement dynamics of seasonal settlement classes must be determined to establish a relationship between puerulus abundance and subsequent fishery yield. Pueruli settle in various shallow-water habitats, including masses of the red alga *Laurencia*, algal-covered mangrove roots, and colonies of the bryozoan, *Bugula*. Settlement habitats of 0.04–2 ha can produce 1906–3913 juveniles (20 mm carapace length) annually. Management must protect these critical habitats to assure productivity of the spiny lobster fishery.

L'établissement sur le fond des larves puerulus de la langouste *Panulirus argus* se produit toute l'année dans le sud de la Floride, mais les tendances saisonnières présentent des incohérences. Il se produit couramment au printemps des pics de recrutement, mais on en observe parfois à d'autres saisons. Il est nécessaire de déterminer la dynamique des classes saisonnières après établissement sur le fond afin de définir la relation entre l'abondance des puerulus et la production halieutique subséquente. Les puerulus s'installent dans divers habitats d'eau peu profonde, qui présentent des masses de l'algue rouge *Laurencia*, des racines de la mangrove couvertes d'algues ou des colonies du bryozoaire *Bugula*. Des habitats de 0,04 à 2 ha peuvent produire chaque année 1 906 à 3 913 juvéniles (20 mm de longueur de la carapace). La gestion doit protéger ces habitats critiques afin d'assurer la productivité de la pêche de la langouste.

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The puerulus of the Florida spiny lobster, *Panulirus argus*, is a free-swimming stage which links the planktonic and benthic phases in the life cycle. Following offshore metamorphosis from the final larval stage, pueruli migrate shoreward and settle in various nearshore habitats (Sweat 1968; Witham et al. 1968; Lyons 1980). After settlement, pueruli acquire camouflaging pigmentation rapidly and molt into the juvenile form within a few days. Numbers of pueruli arriving in the nearshore environment have been estimated for several spiny lobster species by measuring settlement rates on floating collectors (Serfling and Ford 1975; Phillips and Hall 1978; Little and Milano 1980). When puerulus abundance estimates are related to other population characteristics, e.g. previous spawning and subsequent adult abundance, a comprehensive picture of spiny lobster population dynamics can be obtained. This has been done with some success for *Panulirus cygnus*, the rock lobster of Western Australia (Morgan et al. 1982).

Knowledge of seasonal patterns of recruitment is fundamental to puerulus monitoring programs. For example, recruitment of *P. cygnus* pueruli occurs principally from September through January, and abundance estimates are derived from settlement on collectors deployed during that period (Phillips and Hall 1978; Morgan et al. 1982). In this paper, I review collector settlement data to determine the seasonal nature of *P. argus* puerulus recruitment. Implications of these findings with respect to developing a puerulus monitoring program in south Florida are discussed.

Pueruli collectors, although valuable as quantitative sampling devices, reveal very little about habitat requirements and postsettlement ecology of recently settled lobsters. Therefore, a review of the postsettlement period for *P. argus* is included to provide a total perspective regarding this phase in the life cycle. Young benthic lobsters demonstrate behaviors and habitat requirements different from older stages. Those requirements must be understood to maintain long-term productivity of nursery habitat in light of increasing human disruption of south Florida coastline.

## Settlement on Collectors

Recruitment of pueruli along the southeast Florida coast and in the Florida Keys (Fig. 1) has been studied using collectors placed in nearshore shallows. Collectors typically have consisted of several pages of highly textured webbing material suspended from a float at the surface of the water (Witham et al. 1968; Little and Milano 1980). Most studies have used relatively few collectors. Collector design (e.g. size and number of pages) and sampling frequency have varied. Consequently, geographic and year-to-year differences in recruitment magnitude are difficult to discern. Varied sampling of few collectors is less of a problem in identifying seasonal trends of

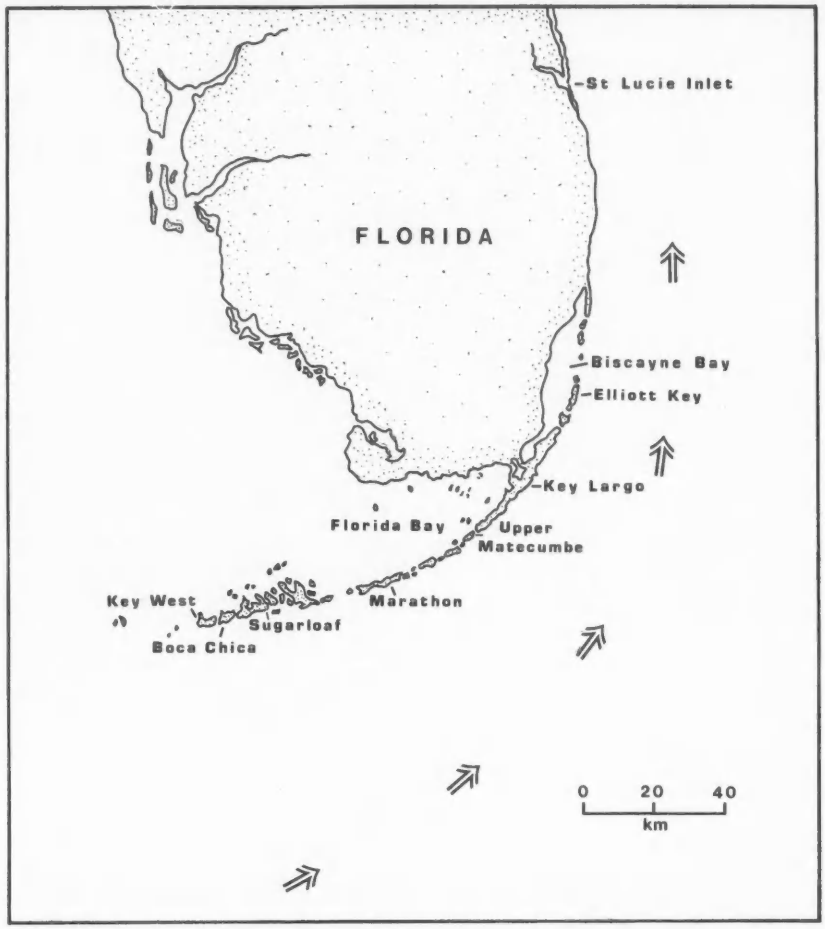


FIG. 1. South Florida locations where puerulus settlement has been studied. Arrows represent approximate location of inshore edge of Florida Current (Gulf Stream).

recruitment. For example, magnitude of settlement differed significantly at three collector stations along Boca Chica Key during 1976–77, but seasonal trends at each station were very similar (Little and Milano 1980). Seasonal trends at Boca Chica Key during 1976–77 were similar to those in 1977–78, despite the fact that sampling was daily during 1976–77 but only once every 3 d during new moon and first quarter lunar phases in 1977–78 (Little and Milano 1980). Based on elaborate statistical tests, Little and Milano (1980) concluded that a single collector should adequately describe relative changes in seasonal abundance of pueruli at a particular station. Phillips and Hall (1978) observed highly variable settlement rates by pueruli of *P. cygnus* on individual collectors at particular sites, but noted that "all collectors at a site indicated similar trends in the level of settlement from month to month and from year to year." Based on these observations, settlement data for *P. argus* reviewed here are considered to accurately reflect seasonal trends of puerulus recruitment. To address the question of seasonal trends more quantitatively, I reformulated the data of Little (1977) and Little and Milano (1980) by summing monthly catch per unit effort (CPUE) values into seasons and expressing seasonal contributions as percentages of total CPUE for each year. Statistical tests were not possible because individual collector data were not always included in original reports.

Collectors were deployed in the Indian River estuary near St. Lucie Inlet from late April 1965 through September 1968 (Witham et al. 1968; Little 1977). Relatively high levels of settlement occurred in spring of 1965, 1967, and 1968 (Fig. 2). High levels of settlement also occurred in August–September 1965 and December 1967. From June through September of 1966 and 1968, freshwater discharges into the estuary by the St. Lucie flood control system reduced salinities to 5–15 ppt, well below the tolerance level of pueruli (Witham et al. 1968; Little 1977). Low settlement levels then may have been caused by salinity reductions rather than limited abundance of pueruli in adjacent oceanic waters.

Additional settlement data were obtained during 1967 at Airport Lagoon and Rest Beach along the southern shore of Key West (Sweat 1968; Little 1977). Puerulus settlement during summer was relatively high at each location (Fig. 3), in contrast with low settlement levels at Indian River estuary

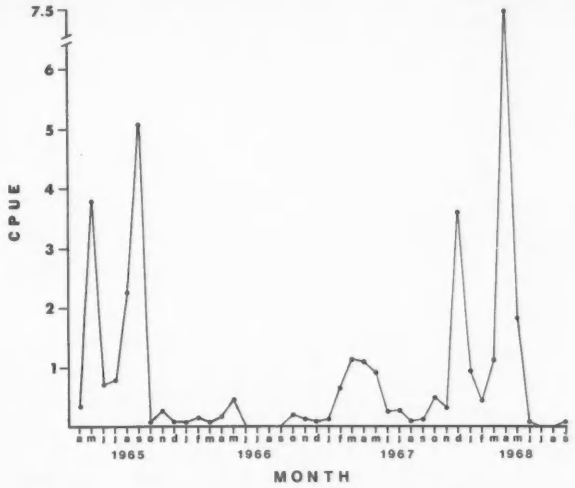


FIG. 2. Monthly CPUE (mean number of pueruli per collector sample) at Indian River estuary, late April 1965 through September 1968. Between three and five collectors were usually sampled. Sampling was irregular through August 1965, daily from September 1965 through September 1967, and 3 times per week thereafter. Derived from Little (1977).

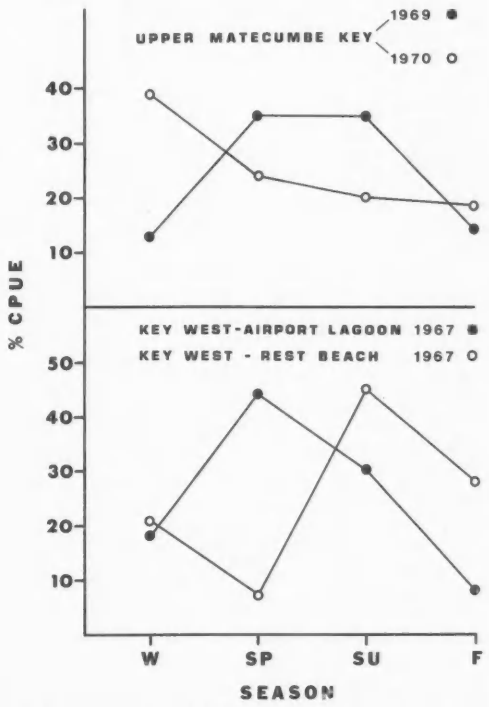


FIG. 3. Percentage of total CPUE (mean number of pueruli per collector sample) by season at Key West (1967) and Upper Matecumbe Key (1969, 1970). Key West data based on single collectors sampled every 2–4 d; 337 pueruli were caught at Airport Lagoon and 235 at Rest Beach. Upper Matecumbe Key data based on one to five collectors (usually greater than three) sampled daily during new moon and first quarter lunar phases; 339 pueruli were caught in 1969 and 485 in 1970. Derived from Little (1977).

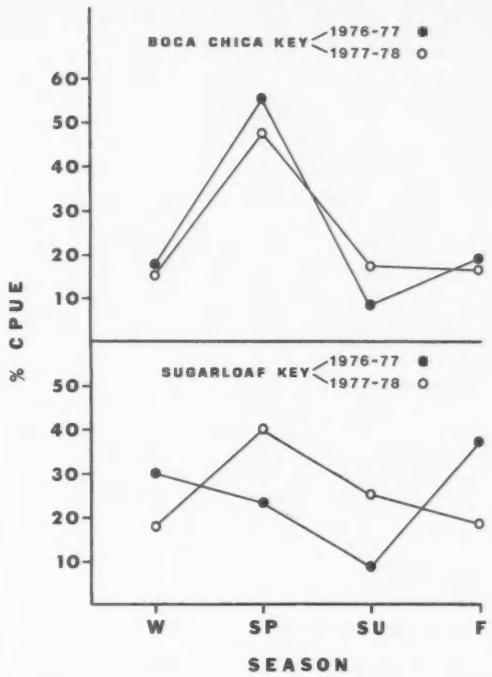


FIG. 4. Percentage of total CPUE (mean number of pueruli per collector per day) by season at two locations in the lower Florida Keys, June 1976 through May 1977 and October 1977 through September 1978. Boca Chica Key 1976–77 data based on nine collectors sampled daily. Sugarloaf Key 1976–77 data based on three collectors sampled twice weekly. Data for each location during 1977–78 based on 18 collectors sampled every 3 d during new moon and first quarter lunar phases. More than 1000 pueruli were caught each year at each location. Derived from Little and Milano (1980).

during that summer (Fig. 2). Inexplicably, high settlement during spring was apparent at Airport Lagoon but not at Rest Beach.

Collectors at Upper Matecumbe Key showed peak settlement during spring–summer 1969 and winter 1970 (Fig. 3). Moderate levels of settlement were evident during spring through fall 1970. Settlement during fall, although less than other seasons, still represented 18% of total CPUE for that year.

The Florida Department of Natural Resources (FDNR) conducted extensive settlement studies in the lower Florida Keys from March 1976 through September 1978 (Little and Milano 1980). Seasonal patterns of puerulus settlement at Boca Chica Key were very similar between 1976–77 and 1977–78 and showed definite spring peaks (Fig. 4). A less pronounced peak occurred at Sugarloaf Key during spring 1977–78, but, in 1976–77, greatest settlement occurred there during fall and winter. Thus, moderate levels of settlement occurred during most seasons at Sugarloaf Key.

Between 20 and 40 collectors were sampled on a weekly basis from April 1978 to June 1979 at Elliott Key (Menzies 1981). Settlement rates (average number of pueruli per collector per week) were relatively high in spring 1978, declined through summer and fall, and then increased during winter and spring 1979.

These data provide strong evidence that recruitment of *P.*

*argus* pueruli to south Florida occurs throughout the year. No consistent seasonal trend is apparent. Peak influxes of pueruli commonly occur in spring, but less than 50% of total annual settlement generally occurs then (Fig. 3 and 4). Contributions during other seasons are highly variable; heavy influx may occur during winter, summer, or fall. Also, seasonal patterns of recruitment may differ between locations within a year, and between years at a location. In contrast, recruitment of *P. cygnus* is confined largely to September through January (spring–summer) with virtually no settlement between May and August (Phillips and Hall 1978).

Year-round puerulus recruitment to south Florida, characterized by substantial seasonal and geographic variability, has important implications for establishing a relationship between puerulus abundance and subsequent fishery yield. Puerulus abundance estimates will require year-round sampling with collectors at several locations throughout the range of the fishery. After quantification of puerulus influx, relative contributions of many settlement classes to later harvest will have to be estimated. Estimates will be complicated greatly because settlement classes within a given year will enter the harvestable stock during more than one fishing year. Available growth data are not sufficiently precise to define such relationships accurately. Estimates of postsettlement periods required to attain harvestable size (76 mm carapace length (CL)) range from 20 to 40 mo and depend on several factors (Lyons et al. 1981; Marx and Herrnkind 1986). Disparate growth rates occur among lobsters within single recruitment cohorts (Witham et al. 1968). Juvenile lobsters grow more rapidly in Florida Bay than in Biscayne Bay (Davis and Dodrill 1980). Injured lobsters, prevalent in the Keys population due to intensive handling by commercial and recreational fishermen, grow slower than uninjured lobsters (Davis 1981; Hunt and Lyons 1986). Moreover, entry of a large segment of the juvenile population into harvestable size classes is delayed or prevented due to the fishery practice of using sublegal-sized lobsters as social attractants in traps (Hunt et al. 1986). These complications are compounded further by seasonal influences on growth (Davis 1981; Hunt and Lyons 1986), physical disturbance to benthic substrates (Little and Milano 1980), and fluctuating availability of puerulus settlement habitat (Josselyn 1977; Thorhaug and Roessler 1977; Marx and Herrnkind 1985a). Such influences could cause disproportionate contributions by certain settlement classes. Relating puerulus abundance estimates to later fishery harvest will require that postsettlement dynamics of seasonal settlement classes be determined.

Demonstrating year-to-year fluctuation in the magnitude of *P. argus* puerulus recruitment has not been possible due to sampling inconsistencies and lack of long-term sampling at fixed locations. However, variability within the limited periods of observations implicates puerulus recruitment levels as a possible factor regulating harvestable stock abundance. Mean annual settlement at Indian River estuary increased from 0.07 to 1.38 pueruli per collector sample (nearly 20 times) between 1966 and 1968 (Little 1977). Magnitude of recruitment peaks at Whale Harbor Bridge (upper Florida Keys; plankton net samples) increased steadily between 1966 and 1968 (Sweat 1968), perhaps reflecting a similar trend there. Settlement at Sugarloaf Key was relatively constant between 1976–77 and 1977–78 but increased nearly 3 times at Boca Chica Key during that period (Table 1). Similar variation in recruitment magnitude was observed for *P. cygnus* between 1969 and 1979 (Morgan et al. 1982). Such variation was correlated positively with subsequent fishery yield. Variable landings in the Florida *P. argus* fishery (Gulf of Mexico and South Atlantic Fishery Management Councils 1982) may also be related to fluctuating levels of puerulus recruitment. Dependence of harvest on magnitude of puerulus recruitment is supported by evidence that food and shelter are not limiting to juvenile populations (Davis 1979; Marx and Herrnkind 1985a).

TABLE 1. Mean number of pueruli per collector per day, new moon and first quarter lunar periods only, at two locations in the lower Florida Keys, June 1976 through May 1977 and October 1977 through September 1978. Derived from Little and Milano (1980).

| Location | 1976–77 | | 1977–78, observed |
|---|---|---|---|
| | Observed | Adjusted[a] | |
| Boca Chica Key | 0.73 | 1.17 | 3.33 |
| Sugarloaf Key | 2.36 | 4.48 | 5.08 |

[a]For comparative purposes, 1976–77 catches were adjusted upward because in 1977–78, more effective collectors were used and data included pigmented pueruli. See Little and Milano (1980).

TABLE 2. Mean distance from shore (±1 SD) of the inshore edge of the Florida Current (Gulf Stream) at various locations between Key West and St. Lucie Inlet. Data based on 7 yr of continuous monitoring. Adapted from Gaby and Baig (1983).

| Location | Mean distance (km) |
|---|---|
| Key West | 77±20 |
| Marathon | 60±16 |
| Key Largo | 45±12 |
| St. Lucie Inlet | 22±6 |

Spawning characteristics of *P. argus* populations that supply Florida with larvae, combined with fluctuations in current systems involved in larval transport, probably account for some recruitment variability. Larvae upon which Florida's lobster population depends may come from the Caribbean, where spawning occurs throughout the year, or from local populations which spawn principally during late spring and summer (Lyons 1981; Lyons et al. 1981; Gregory et al. 1982). Evidence confirming either source is not conclusive (Lyons 1986). Possible mechanisms involved in transporting "foreign" larvae to south Florida and/or retaining locally spawned larvae in oceanic waters off the south Florida coast are poorly understood. Interactions between major currents of the Caribbean Sea and the Gulf of Mexico are complex, and currents off the Florida coast vary seasonally and are characterized by periodic countercurrents and eddies (Little 1977; Maul 1977; Menzies and Kerrigan 1979; Gaby and Baig 1983).

Recruitment variability also may result from changing hydrodynamic conditions rather than fluctuation in larval abundance, per se. Sims and Ingle (1967) found no significant changes in late-stage larval abundance at several locations between the Yucatan Straits and the southeast Florida coast, either from month to month or by location. Richards and Potthoff (1981) reported that late-stage palinurid larvae were present off Florida throughout the year. Those observations, combined with the fact that peak influxes of pueruli within a season

frequently are confined to a single month (Fig. 2; Little 1977; Little and Milano 1980), suggest that major recruitment events depend on facilitative hydrodynamic conditions. In particular, recruitment is likely influenced by distances pueruli must transit to reach coastal habitats. If most late-stage larvae are entrained in the Florida Current (Lewis 1951; Sims and Ingle 1967; Sweat 1968; Witham et al. 1968), minimum distances to coastal habitat vary from less than 20 to nearly 100 km (Table 2). It is difficult to assess the impact of such variability on recruitment because of uncertainty regarding both the duration of the puerulus stage (Lyons 1980) and the role of passive transport mechanisms (Shanks 1983, 1985; Staples and Vance 1985) in shoreward migration.

## Settlement in Natural Habitat

Small lobsters (settlement occurs at 6 mm CL) occupy habitats well suited to their size, cryptic coloration, and seclusive behavior. Recently settled juveniles (6–15 mm CL) are found within patches of *Laurencia* spp., a red macroalgae, in shallow water throughout bayside areas of the Florida Keys (Marx and Herrnkind 1985a). Small patches of *Laurencia* support large numbers of gastropods, crustaceans, and other fauna preyed upon by young lobsters. Attraction to, and residency time within, *Laurencia* patches depend on food availability (Marx and Herrnkind 1985b; W. F. Herrnkind and M. J. Butler, IV, Department of Biology, Florida State University, Tallahassee, FL, unpubl. data). Other rhodophycean algae which occur on mangrove roots or as unattached patches among seagrasses are occupied by similarly sized juveniles in the Indian River estuary (Witham et al. 1964). Recently settled juveniles in the Indian River estuary also inhabit colonies of *Bugula neritima*, a reddish-brown bryozoan that forms large bushy masses rich with epifauna (W. G. Lyons, FDNR, 100 8th Ave. SE, St. Petersburg, FL, pers. comm.). Andree (1981) found young juveniles in crevices covered by algae, principally *Laurencia*, along rocky shorelines of Biscayne Bay. These lobsters, slightly older than those previously described, may have settled initially in the *Laurencia* and then moved into the crevices. Such transitions have been observed in other algal habitats (Marx and Herrnkind 1985a). These observations indicate that young benthic lobsters use a variety of qualitatively similar habitats that provide camouflage, shelter, and abundant food.

*Laurencia* is an especially important habitat for young benthic *P. argus*. It is abundant throughout shallow bays of south Florida (Tabb et al. 1962; Hudson et al. 1970; Taylor 1972; Josselyn 1977; Thorhaug and Roessler 1977) and is the second most abundant macrophyte, exceeded only by turtle grass, *Thalassia testudinum*, in Florida Bay (J. Zieman, University of Virginia, Charlottesville, VA, pers. comm.). Although settlement habitats described by Marx and Herrnkind (1985a) and Andree (1981) were adjacent to rocky shorelines, *Laurencia* habitat harboring recently settled *P. argus* has since been located at several locations in central Florida Bay (J. M. Marx, pers. obs.). In addition, recently settled juveniles are found regularly in bycatch of shrimp trawlers in central Biscayne Bay (Eldred et al. 1972; Davis 1979). Juvenile lobster bycatch is greatest from trawls over hard bottom areas with sponges, gorgonians, and algae, including *Laurencia* (S. W. Andree, Florida Sea Grant, Tallahassee, FL, pers. comm.). These hard bottom habitats closely resemble habitats for young juveniles described by Marx and Herrnkind (1985a).

The cumulative productivity of other settlement habitats may be significant when *Laurencia* is not available. Many pueruli must spend considerable time in the nearshore oceanside environment prior to "finding" or being entrained in channels that provide access to bayside areas where *Laurencia* is abundant. Occurrence of pueruli in such channels has been documented by Sweat (1968). Limits to the duration of delayed metamorphosis (Lyons 1980) and declining selectivity associated with increasing age (Crisp 1974) may force some pueruli to settle in habitats other than *Laurencia*. Constraints on habitat selectivity may be most severe in the upper Keys, where approximately 40 km of unbroken shoreline impedes entry into Florida Bay. Importance of oceanside habitats in such areas should be investigated.

Recently settled juveniles are agonistic and solitary, and tend to be dispersed widely within habitats (Andree 1981; Marx and Herrnkind 1985a). Solitary dwelling, which allows exploitation of the dispersed food and shelter characteristic of algal-dominated habitat (sensu Brown 1964), is a means of maximizing growth while minimizing predatory risk. By maintaining exclusive access to an algal patch, young juveniles likely reduce the necessity to move between patches, thereby minimizing both predator exposure and energy expenditure. Predation rates on recently settled *P. argus* in exposed substrates are significantly greater than rates on juveniles within algae (W. F. Herrnkind and M. J. Butler, IV, unpubl. data). Any mechanism reducing movement between algal patches thus would appear to be protective. Dispersed spacing results passively from chance encounters between lobsters (sensu Stimson 1973; Marx and Herrnkind 1985a) or from the scattered distribution of settling pueruli. Either way, energetic costs of maintaining a dispersed distribution are minimal, thus enhancing net energetic gains (Brown 1964).

Despite the dispersed distribution of recently settled lobsters, small areas of habitat can produce many juveniles annually (Table 3). High productivity is due to year-round puerulus recruitment and rapid postsettlement growth (Marx and Herrnkind 1985a). Substantial productivity can occur at densities as low as 0.03 lobsters/$m^2$ where habitat is relatively abundant. Thus, meaningful productivity estimates require that density estimates be augmented by assessments of habitat availability. Sampling for early benthic stages should quantify settlement habitat as well as lobster density. Investigators should not expect a priori to find "high" densities of young juveniles (<20 mm CL) in habitats they suspect to be important.

How much algal habitat is required to support the south Florida lobster fishery? The fishery harvests about 6 million lobsters annually (J. E. Powers and S. P. Bannerot, National Marine Fisheries Service summary to Gulf of Mexico Fishery Management Council, May 1984). Assuming annual mortality of 35% (Olsen and Koblic 1975; Waugh 1981) and 2 yr to grow from 20 mm CL to harvestable size (Lyons et al. 1981; Marx and Herrnkind 1986), about 15 million juveniles of 20 mm CL are required to yield 6 million harvestable lobsters. At postsettlement densities of only 0.03/$m^2$, 1 ha of *Laurencia* habitat can produce 1193 juveniles of 20 mm CL annually (Table 3; (1906 + 2864)/2 = 2385; 2385/2 ha = 1193). Thus, about 12 600 ha of *Laurencia* habitat is required to produce 15 million juveniles annually. This amount of habitat represents only 4% of the bottom area available in Florida Bay, Biscayne Bay, and bayside areas of the lower Florida Keys (total bottom area 300 000 ha; see Davis and Dodrill 1980 for partial estimates).

TABLE 3. Estimated annual production of 20 mm CL juveniles by two habitats in the upper and middle Florida Keys at growth rates of 4 or 6 mm CL/mo. Based on model by Marx and Herrnkind (1985a).

| Location | Mean density/$m^2$ | Habitat area (ha) | Growth | Productivity per habitat |
|---|---|---|---|---|
| Elliott Key[a] | 1.9 | 0.04[c] | 4[d] | 2607 |
| | | | 6[e] | 3913 |
| Burnt Point[b] | 0.03 | 2 | 4 | 1906 |
| | | | 6 | 2864 |

[a]Andree (1981).
[b]Marx and Herrnkind (1985a); located near Marathon.
[c]S. W. Andree (pers. comm.).
[d]Witham et al. (1968).
[e]Calinski (1985).

Where higher lobster densities occur (Andree 1981; Table 3), only 0.0007% of total bottom area need serve as settlement habitat to produce 15 million juveniles annually. These extrapolations illustrate that sparsely populated settlement habitats need comprise only a small fraction of total bottom area to support a large fishery.

## Synopsis

Considerable attention has focused on the issue of larval origins (Menzies and Kerrigan 1979; Menzies 1981, 1982; Lyons 1981), but the stock recruitment process deserves equal emphasis. Is there a relationship between levels of puerulus influx and subsequent fishery yield, and, if so, what factors regulate seasonal occurrence and abundance of pueruli? Are these factors responsive to management, e.g. the protection of spawning stock, or do they work in a manner not influenced by fishery regulation? Answering such questions will be a complex undertaking due to year-round recruitment of pueruli, but definitive answers are required to enhance management capabilities.

Selective habitat use by early benthic *P. argus* represents an additional phase of habitat partitioning manifest among juveniles prior to ontogenetic migration of subadults to offshore reefs (Davis 1979; Herrnkind 1980; Kanciruk 1980). Such partitioning indicates that single resource management approaches are not appropriate. Assuring continued productivity of nurseries will require protection of entire inshore systems spanning several community types, e.g. algal beds, seagrass meadows, and hard bottom sponge/gorgonian habitats. How might increased turbidity and sedimentation, common by-products of coastal development, affect these habitats? Cumulative effects of even small-scale disruptions may be substantial because small, localized puerulus settlement habitats are productive. Evaluation of human development impacts should be done within this context.

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## References

ANDREE, S. W. 1981. Locomotory activity patterns and food items of benthic postlarval spiny lobsters, *Panulirus argus*. M.S. thesis, Florida State University, Tallahassee, FL. 50 p.

BROWN, J. L. 1964. The evolution of diversity in avian territorial systems. Wilson Bull. 76: 160–169.

CALINSKI, M. D. 1985. Settlement, growth, and survival of puerulus to juvenile stage spiny lobsters in artificial nursery habitats and potential application of such habitats to Florida's fishery, p. 1–3. *In* W. F. Herrnkind [ed.] Proceedings of a workshop on Florida spiny lobster research and management. Florida Sea Grant Tech. Pap. 32.

CRISP, D. J. 1974. Factors influencing settlement of marine invertebrate larvae, p. 177–265. *In* P. T. Grant and A. M. Mackie [ed.] Chemoreception in marine organisms. Academic Press, New York, NY.

DAVIS, G. E. 1979. Management recommendations for juvenile spiny lobsters, *Panulirus argus*, in Biscayne National Monument, Florida. So. Fla. Res. Cent. Rep. M-530, U.S. National Park Service. 32 p.

1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fish. Bull. (U.S.) 78: 979–984.

DAVIS, G. E., AND J. W. DODRILL. 1980. Marine parks and sanctuaries for spiny lobster fishery management. Proc. Gulf Caribb. Fish. Inst. 32: 194–207.

ELDRED, B., C. R. FUTCH, AND R. M. INGLE. 1972. Studies of juvenile spiny lobsters, *Panulirus argus*, in Biscayne Bay, Florida. Fla. Dep. Nat. Resour. Mar. Res. Lab. Spec. Sci. Rep. 35: 15 p.

GABY, D., AND S. BAIG. 1983. Gulf stream variability and width. Mariners Weather Log 27: 133–134.

GREGORY, D. R. JR., R. F. LABISKY, AND C. L. COMBS. 1982. Reproductive dynamics of the spiny lobster *Panulirus argus* in south Florida. Trans. Am. Fish. Soc. 111: 575–584.

GULF OF MEXICO AND SOUTH ATLANTIC FISHERY MANAGEMENT COUNCILS. 1982. Fishery management plan, environmental impact statement and regulatory analysis for spiny lobster in the Gulf of Mexico and South Atlantic. U.S. Department of Commerce, National Oceanic and Atmospheric Administration, Washington, DC.

HERRNKIND, W. F. 1980. Spiny lobsters: patterns of movement, p. 349–407. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

HUDSON, J. H., D. M. ALLEN, AND T. J. COSTELLO. 1970. The flora and fauna of a basin in central Florida Bay. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. No. 604: 14 p.

HUNT, J. H., AND W. G. LYONS. 1986. Factors affecting growth and maturation of spiny lobsters, *Panulirus argus*, in the Florida Keys. Can. J. Fish. Aquat. Sci. 43: 2243–2247.

HUNT, J. H., W. G. LYONS, AND F. S. KENNEDY, JR. 1986. Effects of exposure and confinement on spiny lobsters, *Panulirus argus*, used as attractants in the Florida trap fishery. Fish. Bull. (U.S.). 84: 69–76.

JOSSELYN, M. N. 1977. Seasonal changes in the distribution and growth of *Laurencia poitei* (Rhodophyceae, Ceramiales) in a subtropical lagoon. Aquat. Bot. 3: 217–229.

KANCIRUK, P. 1980. Ecology of juvenile and adult Palinuridae (spiny lobsters), p. 59–92. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

LEWIS, J. B. 1951. The phyllosoma larvae of the spiny lobster, *Panulirus argus*. Bull. Mar. Sci. 1: 89–103.

LITTLE, E. J. JR. 1977. Observations on recruitment of postlarval spiny lobsters, *Panulirus argus*, to the south Florida coast. Fla. Mar. Res. Publ. No. 29: 35 p.

LITTLE, E. J. JR., AND G. R. MILANO. 1980. Techniques to monitor recruitment of postlarval spiny lobsters, *Panulirus argus*, to the Florida Keys. Fla. Mar. Res. Publ. No. 37: 16 p.

LYONS, W. G. 1980. The postlarval stage of scyllaridean lobsters. Fisheries 5(4): 47–49.

1981. Possible sources of Florida's spiny lobster population. Proc. Gulf Caribb. Fish. Inst. 33: 253–266.

1986. Problems and perspectives regarding recruitment of spiny lobsters, *Panulirus argus*, to the south Florida fishery. Can. J. Fish. Aquat. Sci. 43: 2099–2106.

LYONS, W. G., D. G. BARBER, S. M. FOSTER, F. S. KENNEDY, JR., AND G. R. MILANO. 1981. The spiny lobster, *Panulirus argus*, in the middle and upper Florida Keys: population structure, seasonal dynamics, and reproduction. Fla. Mar. Res. Publ. No. 38: 38 p.

MARX, J. M., AND W. F. HERRNKIND. 1985a. Macroalgae (Rhodophyta: *Laurencia* spp.) as habitat for young juvenile spiny lobsters, *Panulirus argus*. Bull. Mar. Sci. 36: 423–431.

1985b. Factors regulating microhabitat use by young juvenile spiny lobsters, *Panulirus argus*: food and shelter. J. Crustacean Biol. 5: 650–657.

1986. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida) — spiny lobster. U.S. Fish Wildl. Serv. FWS-OBS 82/11. U.S. Army Corp. Eng., TR EL-82-4. (In press)

MAUL, G. A. 1977. The annual cycle of the Gulf Loop Current. Part I: Observations during a one-year time series. J. Mar. Res. 35: 29–47.

MENZIES, R. A. 1981. Biochemical population genetics and the spiny lobster larval recruitment problem: an update. Proc. Gulf Caribb. Fish. Inst. 33: 230–243.

1982. Progress and directions of biochemical systematics studies of the Florida spiny lobster, p. 15. *In* W. G. Lyons [ed.] Proceedings of a workshop on Florida spiny lobster research and management. Florida Department of National Resources, Marine Research Laboratory, St. Petersburg, FL.

MENZIES, R. A., AND J. M. KERRIGAN. 1979. Implications of spiny lobster recruitment patterns of the Caribbean — a biochemical genetic approach. Proc. Gulf Caribb. Fish. Inst. 31: 164–178.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia. Fish. Bull. (U.S.) 80: 475–486.

OLSEN, D. A., AND I. G. KOBLIC. 1975. Population dynamics, ecology, and behavior of spiny lobsters, *Panulirus argus*, of St. John, U.S.V.I.: II. Growth and mortality, p. 17–21. *In* S. A. Earle and R. J. Lavenberg [ed.] Results of the Tektite program: coral reef invertebrates and plants. Nat. Hist. Mus. Los Ang. Cty Sci. Bull. 20.

PHILLIPS, B. F., AND N. G. HALL. 1978. Catches of puerulus larvae on collectors as a measure of natural settlement of the western rock lobster *Panulirus cygnus* George. CSIRO Div. Fish. Oceanogr. Rep. No. 98: 18 p.

RICHARDS, W. J., AND T. POTTHOFF. 1981. Distribution and seasonal occurrence of larval pelagic stages of spiny lobsters (Palinuridae, *Panulirus*) in the western tropical Atlantic. Proc. Gulf Caribb. Fish. Inst. 33: 244–252.

SERFLING, S. A., AND R. F. FORD. 1975. Ecological studies on the puerulus larval stage of the California spiny lobster, *Panulirus interruptus*. Fish. Bull. (U.S.) 73: 360–377.

SHANKS, A. L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Mar. Ecol. Prog. Ser. 13: 311–315.

1985. Behavioral basis of internal-wave-induced shoreward transport of megalopae of the crab *Pachygrapsus crassipes*. Mar. Ecol. Prog. Ser. 24: 289–295.

SIMS, H. W. JR., AND R. M. INGLE. 1967. Caribbean recruitment of Florida's spiny lobster population. Q. J. Fla. Acad. Sci. 29: 207–242.

STAPLES, D. J., AND D. J. VANCE. 1985. Short-term and long-term influences on the immigration of postlarval banana prawns, *Penaeus merguiensis*, into a mangrove estuary of the Gulf of Carpentaria, Australia. Mar. Ecol. Prog. Ser. 23: 15–29.

STIMSON, J. 1973. The role of territory in the ecology of the intertidal owl limpet, *Lottia gigantea*. Ecology 54: 1020–1030.

SWEAT, D. E. 1968. Growth and tagging studies on *Panulirus argus* (Latreille) in the Florida Keys. Fla. Board Conserv. Mar. Res. Lab. Tech. Ser. No. 57: 30 p.

TABB, D. C., D. L. DUBROW, AND R. B. MANNING. 1962. The ecology of northern Florida Bay and adjacent estuaries. Fla. State Board Conserv. Tech. Ser. No. 39: 81 p.

TAYLOR, W. R. 1972. Marine algae of the eastern tropical and subtropical coasts of the Americas. University of Michigan Press, Ann Arbor, MI. 870 p.

THORHAUG, A., AND M. ROESSLER. 1977. Seagrass community dynamics in a subtropical estuarine lagoon. Aquaculture 12: 253–277.

WAUGH, G. T. 1981. Management of juvenile spiny lobster (*Panulirus argus*) based on estimated biological parameters from Grand Bahama Island, Bahamas. Proc. Gulf Caribb. Fish. Inst. 33: 271–289.

WITHAM, R., R. M. INGLE, AND E. A. JOYCE, JR. 1968. Physiological and ecological studies of *Panulirus argus* from the St. Lucie estuary. Fla. Board Conserv. Mar. Res. Lab. Tech. Ser. No. 53: 31 p.

WITHAM, R., R. M. INGLE, AND H. W. SIMS, JR. 1964. Notes on postlarvae of *Panulirus argus*. Q. J. Fla. Acad. Sci. 27: 289–297.

# Movements of the Spiny Lobster *Panulirus argus* in South Florida[1]

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Gregory, D. R. Jr., and R. F. Labisky. 1986. Movements of the spiny lobster *Panulirus argus* in south Florida. Can. J. Fish. Aquat. Sci. 43: 2228–2234.

Long-distance movements of the spiny lobster *Panulirus argus* were studied in two Gulf of Mexico habitats (Shallows, Mid-depth) and three Atlantic Ocean habitats (Shallows, Patch Reef, and Deep Reef) in the lower Florida Keys during the mid-1970's. Of 6062 spiny lobsters tagged and released at the five sites between June 1975 and August 1976, 465 of the 771 (13%) lobsters recovered yielded usable movement data. Eighty percent of the tags were recovered within the first 3 mo of the 8 mo commercial fishing season (July 26 – March 31). Directions and rates of movements differed significantly ($P < 0.05$) among sites. Movements from Gulf sites were generally oriented to the west and southwest, toward the Atlantic offshore reefs, at mean displacement velocities of 0.57 km/d (Mid-depth) and 0.24 km/d (Shallows). Movements of lobsters from the Atlantic sites were principally eastward and westward, parallel to the reef line and island chain, at mean displacement velocities of 0.02 km/d (Deep Reef) and 0.05 km/d (Shallows, Patch Reef). The more directed movements of spiny lobsters from Gulf sites may reflect a migration from nursery grounds to the Atlantic reefs, which not only constitute the primary spawning habitat but also exhibit a more stable winter environment than the shallow Gulf. Movements of spiny lobsters within Atlantic waters reflect localized random onshore–offshore dispersal patterns typical within reef environments.

Les déplacements sur de grandes distances de la langouste *Panulirus argus* ont été étudiés, dans la partie inférieure des Keys de Floride, au milieu des années 1970, dans deux habitats du golfe du Mexique (Shallows, Mid-depth) et trois habitats de l'Océan Atlantique (Shallows, Patch Reef et Deep Reef). Sur les 6 062 langoustes marquées et relâchées aux cinq sites entre juin 1975 et août 1976, 465 des 771 (13 %) spécimens récupérés ont fourni des données utilisables sur leurs déplacements. Quatre-vingts pour cent des marques ont été récupérées dans les 3 premiers mois de la saison de pêche de 8 mo (26 juillet – 31 mars). La direction et la vitesse du déplacement différaient de façon importante d'un site à l'autre ($P < 0,05$). Les déplacements à partir des sites du Golfe étaient généralement orientés vers l'ouest et le sud-ouest, vers les récifs de l'Atlantique, et se faisaient à des vitesses moyennes de 0,57 km/j (Mid-depth) et de 0,24 km/j (Shallows). Les déplacements des langoustes à partir des sites de l'Atlantique étaient orientés principalement vers l'est et l'ouest, parallèlement à la ligne des récifs et à la chaîne insulaire, avec des vitesses moyennes de 0,02 km/j (Deep Reef) et de 0,05 km/j (Shallows, Patch Reef). Les déplacements plus nettement orientés des langoustes du Golfe peuvent représenter une migration des nurseries vers les récifs de l'Atlantique qui constituent non seulement le principal habitat de ponte mais présentent aussi un milieu hivernal plus stable que les eaux peu profondes du Golfe. Les déplacements des langoustes dans les eaux de l'Atlantique reflètent des schémas de dispersion à caractère local et aléatoire entre les côtes et le large, qui sont typiques des milieux récifaux.

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An understanding of the migratory habits of an exploited animal species is requisite to rational management (Harden Jones 1968). Such knowledge permits identification of manageable stocks (Cushing 1968), which enables the dynamics of the population to be effectively integrated into sound management practices. As knowledge of migratory habits is gained, the catch per unit effort by fishermen increases due to the more effective deployment of fishing gear along migration routes or in known areas of abundance. Thus, knowledge of population movements not only enhances the conservation of the stock, but also the efficient use of other capital resources such as fuel, labor, and materials.

The migratory habits of the spiny lobster *Panulirus argus* in south Florida have received little attention until the last decade. Qualitative aspects of localized seasonal *P. argus* movements were described initially in the 1920's (Crawford and De Smidt 1922) when the fishery was still in its incipient stages (Labisky et al. 1980). Dawson and Idyll (1951) presented the first quantitative evidence reporting movements of up to 200 km along the south Florida coast. Recent studies of the spiny lobster in south Florida (Davis 1977; Warner et al. 1977; Lyons et al. 1981) have confirmed the earlier reports of both localized and long-distance movements. However, understanding of the factors influencing movement patterns is limited (Herrnkind 1980).

In 1975, a study of the biology of *P. argus* was initiated in the lower Florida Keys (Warner et al. 1977; Gregory et al.

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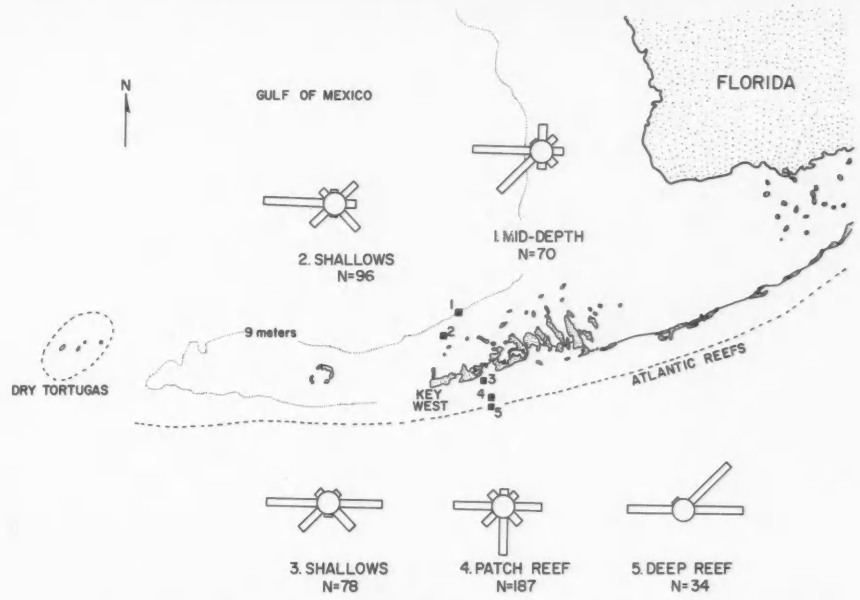


FIG. 1. Movement directions of 465 tagged spiny lobsters released from the five release sites (Gulf of Mexico: 1−2; Atlantic Ocean: 3−5) in the lower Florida Keys, July 1975 − August 1976. Movement directions per site are presented proportionately for the eight depicted compass directions. The study area was located at approximately 24°30′N, 81°30′W.

1982). This paper reports on that segment of the study pertaining to movements of adult and subadult lobsters. Specific objectives were to determine the influences of habitat, season, sex, and size on movements of spiny lobsters in the lower Florida Keys.

## Methods

Spiny lobsters were captured with commercial wooden-slat traps that were placed in five different habitats in the lower Florida Keys (Fig. 1). Two trapping sites were located in the Gulf of Mexico and three in the Atlantic Ocean. Site 1 (Gulf Mid-depth) was located in 7−9 m of water on a hard, flat substrate overlain with sand, typified by a fauna of widely distributed sponges and small corals; Site 2 (Gulf Shallows) in 4−6 m on sand/grass flats with numerous large sponges; Site 3 (Atlantic Shallows) in 5−6 m on sand/mud/grass flats with occasional large coral heads; Site 4 (Atlantic Patch Reef) in 7−12 m on a typical patch reef, interspersed with sand and grass flats; and Site 5 (Atlantic Deep Reef) in 12−27 m on the seaward edge of the offshore reef. Twenty-five traps, positioned at 250-m intervals in a five by five grid (1-km$^2$ area), were used to sample lobsters at each site. Sites 1−4 were sampled weekly for 14 mo (July 1975 − August 1976); Site 5 was sampled weekly for 5 mo (April−August 1976).

Each captured spiny lobster was tagged with a numbered Floy FD-68B tag, measured for carapace length (to the nearest 0.1 mm), and sexed. Carapace length, the middorsal distance from the anterior edge of the cephalothorax (between the supraorbital rostral spines) to the posterior edge of the cephalothorax, was used as the index of body size. In analysis, spiny lobster age groups were defined as juveniles (<70 mm carapace length) and adults (≥70 mm carapace length) because sexual maturity first occurs at 70 mm carapace length (Gregory et al. 1982). The minimum legal size limit for spiny lobsters in Florida is 76.2 mm carapace length.

Recovery of tagged lobsters was accomplished through extensive dockside contact with commercial fishermen and the placement of both Spanish and English posters, with tag recovery report forms, in commercial fish houses and dive shops throughout the lower Florida Keys. The fishermen were requested to provide the tagged lobster intact, as well as the data and location of its capture. Recoveries were effected without offering a monetary reward; instead, intensive direct personal contact was used, i.e. the docks were visited a minimum of three times per week.

Movements of lobsters from each tagging site were analyzed separately due to inherent differences in the habitat type at each site. Release and recovery sites of the tagged individuals were plotted to the nearest 0.5 min, which gave an overall plotting error of ±2 km. The data from each release site were analyzed for uniformity (randomness) of directional movement and for differences among sites with respect to direction, days of freedom, distance moved, and rate of movement.

Nonparametric statistical tests were used due to the obvious non-normal nature of the data. The Kruskal−Wallis analysis of variance by ranks method (Siegel 1956) was used to test for differences in distance moved, days of freedom, and rate of movement among sites. The null hypothesis of uniformity of directional movement, between 0 and 360°, from each release site was examined by Rao's test (Batschelet 1981):

$$U = 1/2 \sum_{i=1}^{n} |T_i - 360/n|$$

where $n$ represents the total number of tag recoveries from each release site and $T_i$ represents the $i$th arc length between angles

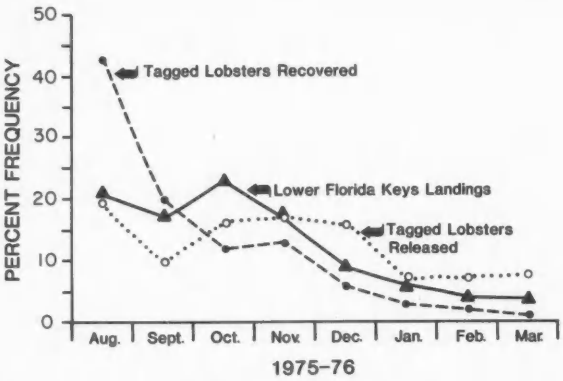


FIG. 2. Monthly percent frequency distribution of tagged lobsters released ($N$ = 2689), tagged lobsters recovered ($N$ = 543), and commercial landings (850 metric tons) in the lower Florida Keys, August 1975 – March 1976.

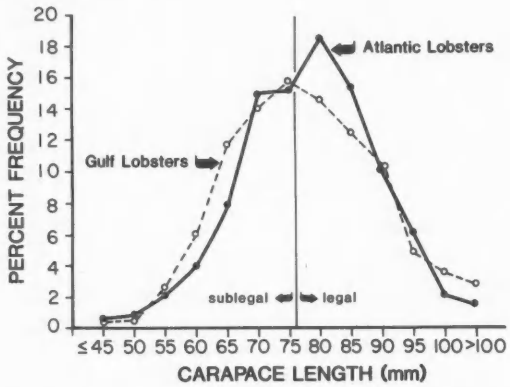


FIG. 3. Percent frequency distribution of carapace length sizes of 6062 spiny lobsters tagged and released at Gulf of Mexico ($N$ = 2951; Sites 1–2) and Atlantic Ocean ($N$ = 3111; Sites 3–5) release sites, lower Florida Keys, July 1975 – August 1976. The separation of sublegal and legal lobsters (76.2 mm carapace length) is denoted by a vertical line.

$i$ and $i + 1$ (arc lengths sum to 360°). If $U$ exceeded a critical value (table L, Batschelet 1981), the null hypothesis of a uniform distribution of lobster movements was rejected. Mean directional variables of lobster movements from each site included the direction of movement ($\theta$), directional displacement velocity ($V$), mean square dispersion coefficient ($a^2$) (Jones 1976), and groundspeed ($s$). The directional values were calculated as follows.

Let

$$x = \sum_{i=1}^{n} r_i \sin \theta_i$$

$$y = \sum_{i=1}^{n} r_i \cos \theta_i.$$

Then

$$\theta = \arctan (x/y)$$

$$V = (x^2 + y^2)^{1/2} \Big/ \sum_{i=1}^{n} t_i$$

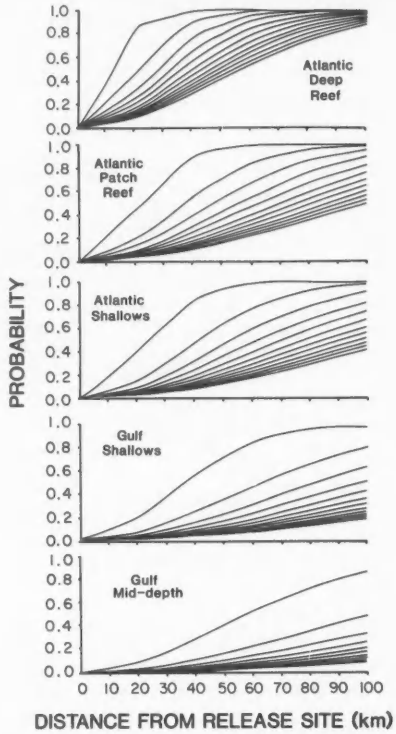


FIG. 4. Probability distributions that tagged spiny lobsters will be found within prescribed distances from release sites in the Gulf of Mexico and Atlantic Ocean during 12 consecutive mo following release. The top curve represents month 1 and the bottom curve month 12.

and

$$a^2 = \left\{ \sum_{i=1}^{n} \left[ r_i^2/t_i - (x^2 + y^2) \Big/ \sum_{i=1}^{n} t_i \right] \right\} \Big/ n$$

$$s = \left\{ \sum_{i=1}^{n} (r_i/t_i) \right\} \Big/ n$$

where $n$ is the total number of tag recoveries from each release site, $r_i$ is the apparent straight-line distance traveled, $t_i$ is the number of days free, and $\theta_i$ is the direction of travel from true north for each recovery site. Cumulative probabilities (Jones 1976) of the proportion of lobsters expected to be found within prescribed distances from each release site during 12 consecutive mo following release were calculated as

$$P(R, t) = 1 - \exp (-R^2/a^2 t_i)$$

where $R = (x^2 + y^2)^{1/2}$, $a^2$ = mean square dispersion coefficient, and $t_i$ = months free ($i$ = 1, 2, 3, . . . ,12). Last, the distribution of directional movements was tested for differences among the five release sites with a multimodal nonparametric test for circular data (Mardia and Spurr 1973):

$$C = 2\left\{ \sum_{i=1}^{c} \left[ \sum_{j=1}^{n_i} \cos (2\pi l r_{ij}/N)^2 + \sum_{j=1}^{n_i} \sin (2\pi l r_{ij}/N)^2 \right] \Big/ n_i \right\}$$

where $N$ is the total number of angles $\theta_{ij}$ ($i$ = 1, 2, 3, . . . , $c$; $j$ = 1, 2, 3, . . . ,$n_i$), $r_{ij}$ is the sequential ranks of the angles in

TABLE 1. Summary of movement parameters of 465 tagged spiny lobsters from Gulf of Mexico and Atlantic Ocean study sites, lower Florida Keys, July 1975 – August 1976. Ranges are in parentheses.

| Movement parameters | Release sites | | | | |
|---|---|---|---|---|---|
| | Gulf | | Atlantic | | |
| | 1 (Mid-depth) | 2 (Shallows) | 3 (Shallows) | 4 (Patch Reef) | 5 (Deep Reef) |
| $N$ | 70 | 96 | 78 | 187 | 34 |
| θ (degrees)[a,b] | 249 | 258 | 241 | 266 | 9 |
| Median distance moved[c] | 16.7 (2–121) | 8.0 (0–101) | 7.3 (1–101) | 3.1 (0–84) | 1.3 (1–38) |
| Median days free[d] | 38 (1–364) | 37 (2–383) | 33 (1–270) | 17 (2–619) | 43 (1–182) |
| Median groundspeed ($s$)[e] | 0.47 (0–14) | 0.25 (0–5) | 0.17 (0–9) | 0.15 (0–7) | 0.05 (0–5) |
| Displacement velocity ($V$) | 0.57 | 0.24 | 0.05 | 0.05 | 0.02 |
| Dispersion ($a^2$) | 40.60 | 16.19 | 6.70 | 5.24 | 1.66 |

[a]Directional distributions of lobster movements from each site were nonuniform. The respective Rao statistics (Batschelet 1981) were $U_1 = 177$, $U_2 = 177$, $U_3 = 179$, $U_4 = 243$, and $U_5 = 264$; all were significant ($P < 0.05$).

[b]Directional distributions of movements among sites were significantly different: $C = 26.85$, df = 8, $P < 0.05$ (Mardia and Spurr 1973).

[c]Significant differences among sites (Kruskal–Wallis test): $\chi^2 = 107$, df = 4, $P < 0.05$.

[d]Significant differences among sites (Kruskal–Wallis test): $\chi^2 = 74$, df = 4, $P < 0.05$.

[e]Significant differences among sites (Kruskal–Wallis test): $\chi^2 = 58$, df = 4, $P < 0.05$.

TABLE 2. Log-linear likelihood ratio chi-square ($G^2$) values for hierarchial models for tests of independence for 461 spiny lobsters (4 lobsters from the Gulf Shallows site were recovered within the release site) recovered among release sites, sex (female, male), age (adult = ≥70 mm; juvenile = <70 mm), and direction of movement (north, east, south, west). Each frequency cell was increased by the addition of 0.5 prior to analysis. Probabilities < 0.05 were considered statistically significant and are indicated by an asterisk.

| Model[a] | df | Release sites | | | | | |
|---|---|---|---|---|---|---|---|
| | | Gulf | | Atlantic | | | |
| | | 1 (Mid-depth) | 2 (Shallows) | 3 (Shallows) | 4 (Patch Reef) | 5 (Deep Reef) | All sites |
| Direction (D) | 12 | 41* | 73* | 38* | 117* | 21* | 244* |
| Sex (S) | 14 | 90* | 118* | 75* | 155* | 34* | 371* |
| Age (A) | 14 | 62* | 82* | 55* | 54* | 19 | 150* |
| D, S, A | 10 | 12 | 32* | 10 | 12 | 7 | 21* |
| DS | 8 | 37* | 49* | 35* | 114* | 21* | 235* |
| DA | 8 | 7 | 31* | 9 | 11 | 5 | 18* |
| SA | 12 | 59* | 78* | 50* | 50* | 15 | 142* |
| DS, DA | 4 | 3 | 7 | 5 | 8 | 5 | 10* |
| DA, SA | 6 | 4 | 27* | 5 | 7 | 1 | 10 |
| DS, SA | 6 | 5 | 10 | 9 | 10 | 2 | 6 |
| DS, DA, SA | 3 | 1 | 6 | 4 | 6 | 1 | 2 |

[a]A test of full-order models (including factors direction, sex, age, and site) indicated that all three-way ($G^2 = 36$, df = 31, $P = 0.26$) and four-way ($G^2 = 16$, df = 12, $P = 0.19$) interactions were negligible. The effect of site interactions on directional differences was not considered pertinent to the examination of the effects of age and sex on directional movements; therefore, only direction, sex, and age factors were analyzed for significant interaction effect.

the $i$th sample, $l$ is the number of modes in the distribution, and $n_i$ is the number of angles in the $c$th sample (here, $l = 2$ and $c = 5$). Critical values of $C$ for $N > 20$ were tested as a chi-square variable with $2(c - 1)$ degrees of freedom. In this paper, decisions on the acceptance of the null hypotheses were made at the 0.05 level of probability.

## Results

Thirteen percent ($N = 771$) of 6062 spiny lobsters tagged and released at the five sample sites between July 1975 and August 1976 were recovered from July 1975 to August 1977; 543 (70%) of the recoveries were accompanied by date records but only 465 (60%) by date and location information. Tagged lobsters were recovered primarily from the commercial trap fishery (96%); the remainder were recovered by sport divers (3%) and commercial shrimp-trawl fishermen (1%). Eighty percent of all recovered tagged lobsters were recovered within the first 3 mo of the 1975–76 and 1976–77 lobster fishing seasons which extended from July 26 to March 31. The tag recovery rate was correlated with the monthly distribution of landings in the lower Keys (Fig. 2).

TABLE 3. Site-specific analysis of variance models of the effects of sex (female, male) age (juvenile, adult), and direction (north, east, south, west) on groundspeed (natural logarithm transformation) of spiny lobster recoveries. Interaction effects degrees of freedom varied among sites due to either missing data or collinearity. Probabilities < 0.05 were considered significant and are indicated by an asterisk.

| Effect | df | Mean square | *F*-value |
|---|---|---|---|
| Site 1 (Gulf Mid-depth) | | | |
| Sex | 1 | 2.22 | 1.85 |
| Age | 1 | 0.11 | 0.09 |
| Direction | 3 | 9.42 | 7.85* |
| Interactions | 7 | 2.12 | 1.77 |
| Residual | 57 | 1.20 | |
| Site 2 (Gulf Shallows) | | | |
| Sex | 1 | 3.28 | 2.41 |
| Age | 1 | 0.09 | 0.07 |
| Direction | 3 | 3.71 | 2.72* |
| Interactions | 4 | 0.98 | 0.72 |
| Residual | 82 | 1.36 | |
| Site 3 (Atlantic Shallows) | | | |
| Sex | 1 | 0.67 | 0.44 |
| Age | 1 | 5.24 | 3.45 |
| Direction | 3 | 2.10 | 1.38 |
| Interactions | 7 | 2.28 | 1.50 |
| Residual | 65 | 1.52 | |
| Site 4 (Atlantic Patch Reef) | | | |
| Sex | 1 | 0.02 | 0.02 |
| Age | 1 | 28.21 | 23.66* |
| Direction | 3 | 33.15 | 27.80* |
| Interactions | 9 | 2.05 | 1.72 |
| Residual | 172 | 1.19 | |
| Site 5 (Atlantic Deep Reef) | | | |
| Sex | 1 | 2.63 | 1.25 |
| Age | 1 | 1.21 | 0.57 |
| Direction | 2 | 7.50 | 3.55* |
| Interactions | 5 | 0.58 | 0.27 |
| Residual | 24 | 2.11 | |

The size distribution of spiny lobsters captured exhibited habitat related differences (Fig. 3). The mean (±SE) carapace length of 2951 Gulf ($\bar{x}$ = 75.3 ± 0.23 mm) and 3111 Atlantic ($\bar{x}$ = 75.9 ± 0.20 mm) tagged lobsters did not differ significantly ($t$ = 1.90, 6060 df, $P$ = 0.06); however, their variances were significantly different ($F$ = 1.19, 2950 and 3110 df, $P < 0.01$). Both larger- and smaller-sized lobsters occurred more frequently in the Gulf samples (36% ≤ 70.0 mm and 6% > 95 mm) than in the Atlantic samples (31% ≤ 70 mm and 4% > 95 mm).

The directional distributions of spiny lobster movements from the five release sites were significantly nonuniform and site specific (Fig. 1; Table 1). In the Gulf, 61% of the recoveries were to the west and southwest whereas in the Atlantic, movements were bimodally directed; 40% of the Atlantic tagged animals moved west, and 59% moved east. In the Atlantic, lobsters released from the inshore sites moved principally offshore. Lobsters from the Atlantic Deep Reef site either moved parallel to the reef tract or moved inshore in a northeasterly direction. Directional movements of spiny lobsters in the lower Florida Keys were oriented primarily toward the offshore Atlantic reefs.

The directional component of spiny lobster movements varied with age and sex (Table 2). Too few juveniles were recovered to evaluate site-specific differences; consequently, data from all sites were combined for further interpretation. Proportionally more females (52%) than males (41%) moved west, and fewer females (20%) than males (29%) moved east. Differences in directional movements between different age groups were less dissimilar; 46% of both juveniles and adults moved west whereas 30% of the juveniles and 23% of the adults moved east.

The movement parameters distance moved, days free, and groundspeed differed significantly among release sites (Table 1). Both displacement velocity and dispersion indices were greatest for the two Gulf sites; lobsters from the Gulf Mid-depth and Shallows exhibited displacement velocities of 0.57 and 0.24 km/d, respectively, whereas displacement velocities from Atlantic sites ranged from 0.02 (Deep Reef) to 0.05 (Shallows and Patch Reef) km/d. Gulf lobsters also exhibited greater mean square dispersion coefficients than Atlantic lobsters (Table 1); thus, the probability of Gulf lobsters remaining near their release site was substantially lower than the corresponding probabilities for Atlantic lobsters (Fig. 4). Therefore, within a given time period, Gulf lobsters moved further and with greater directedness than Atlantic lobsters, which exhibited more localized movements.

Lobster groundspeeds within each release site did not differ significantly between females and males, and only for the Atlantic Patch Reef did groundspeeds differ between juveniles ($s$ = 0.5 ± 0.06 km/d) and adults ($s$ = 0.2 ± 0.09 km/d) (Tables 3 and 4). However, groundspeeds varied significantly with direction at all release sites except the Atlantic Shallows. In the Gulf, groundspeeds were greatest toward the south ($s$ = 2.3 km/d, Mid-depth; $s$ = 0.7 km/d, Shallows) and west ($s$ = 1.3 km/d, Mid-depth; $s$ = 0.7 km/d, Shallows). In the Atlantic, groundspeeds were more variable; movement rates were slowest to the south (offshore) and fastest to the east ($s$ = 0.5 km/d, Patch Reef; $s$ = 0.6 km/d, Deep Reef) and west ($s$ = 0.8 km/d, Patch Reef).

## Discussion

Migrations of tagged animals can be inferred directly only if catch and effort are distributed uniformly in all recovery areas (Saila 1961). However, uniform distribution of effort occurs rarely, and the possibility exists that randomly moving tagged animals captured by a fishery, which differs in spatial and temporal intensity, could appear to exhibit directed movements. Virtually no documented information exists on the monthly spatial distribution of fishing effort during the fishing season for spiny lobsters in the south Florida fishery. However, the exploitation rate in 1975 was about 80% (Anonymous 1982) and was effected by 823 vessels fishing 520 000 traps (Labisky et al. 1980); therefore, the fishing grounds probably were saturated sufficiently with traps to reflect lobster movements accurately, particularly those movements that occurred during the first 3 mo of the fishing season, during which time 80% of all tag recoveries occurred (Fig. 2). About 50% of all tag recoveries occurred within 1 mo of freedom and 90% were recovered within 3 mo of freedom.

The high percentage of tag recoveries made within 3 mo of release was most likely due to (1) a high tag loss rate during first molt subsequent to tagging, (2) movement out of the fishery, and (3) intense fishing pressure. Although no estimates

TABLE 4. Average groundspeed ($s$ in km/d) of 461 tagged spiny lobster recoveries by age, sex, and direction of movement for each release site.

| | Release site | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Gulf | | | | | | Atlantic | | | | | | | | |
| | 1 (Mid-depth) | | | 2 (Shallows)[a] | | | 3 (Shallows) | | | 4 (Patch Reef) | | | 5 (Deep Reef) | | |
| Parameter | $N$ | $\bar{x}$ | SD | $N$ | $\bar{x}$ | SD | $N$ | $\bar{x}$ | SD | $N$ | $\bar{x}$ | SD | $N$ | $\bar{x}$ | SD |
| Sex | | | | | | | | | | | | | | | |
| Female | 32 | 1.7 | 2.72 | 37 | 0.5 | 0.57 | 30 | 0.4 | 0.55 | 104 | 0.5 | 0.88 | 16 | 0.1 | 0.13 |
| Male | 38 | 0.8 | 0.80 | 55 | 0.7 | 0.92 | 48 | 0.6 | 1.44 | 83 | 0.5 | 0.58 | 18 | 0.5 | 1.15 |
| Age | | | | | | | | | | | | | | | |
| Juvenile | 12 | 0.8 | 0.85 | 16 | 0.4 | 0.38 | 17 | 0.2 | 0.18 | 26 | 0.2 | 0.48 | 5 | 0.1 | 0.02 |
| Adult | 58 | 1.3 | 2.12 | 76 | 0.6 | 0.86 | 61 | 0.6 | 1.32 | 161 | 0.5 | 0.79 | 29 | 0.3 | 0.92 |
| Direction | | | | | | | | | | | | | | | |
| North | 7 | 0.5 | 1.06 | 5 | 0.2 | 0.08 | 3 | 0.2 | 0.19 | 16 | 0.5 | 0.42 | 12 | 0.1 | 0.05 |
| East | 9 | 0.5 | 0.45 | 24 | 0.5 | 0.72 | 27 | 0.3 | 0.25 | 40 | 0.5 | 0.43 | 12 | 0.6 | 1.39 |
| South | 7 | 2.3 | 5.27 | 12 | 0.7 | 0.97 | 9 | 0.2 | 0.20 | 65 | 0.1 | 0.11 | 0 | — | — |
| West | 47 | 1.3 | 1.27 | 51 | 0.7 | 0.83 | 39 | 0.8 | 1.62 | 66 | 0.8 | 1.11 | 10 | 0.1 | 0.14 |
| Overall | 70 | 1.2 | 2.00 | 92 | 0.6 | 0.80 | 78 | 0.5 | 1.18 | 187 | 0.5 | 0.76 | 34 | 0.3 | 0.85 |

[a]Four lobsters recovered within release site are excluded.

of tag loss rates are available from the current study, Davis (1978) reported a 4% tag loss per month of freedom with similarly tagged spiny lobsters ranging in size from 34 to 84 mm carapace length. Some movements out of the fishery probably occurred because the fishery is constrained to shallow waters (<30 m) by the Gulf Stream currents to the south and west and by the shrimp fishery to the northwest; however, the extent of these movements is unknown. The intense exploitation rate probably accounted for the major proportion of short-term tag recoveries, particularly since exploitation was concentrated principally within the first 3 mo of the 8-mo (July 26 – March 31) fishing season (Fig. 2). Consequently, the overall pattern of movements described in this paper represents short-term movements that occur during the open fishing season.

A general pattern of spiny lobster movements within the lower Florida Keys has emerged. Lobster movements in the Gulf were predominantly to the west and southwest (Fig. 1) and were effected with velocities significantly greater than those of Atlantic lobsters, which exhibited more localized movements — moving not only slower but also shorter distances and with greater multidirectional dispersal (Table 1). Although the island chain to the south of the Gulf sites seemingly represents a physical barrier, Gulf lobsters moved through the tidal channels into the Atlantic. In contrast, no comparable movements from the Atlantic to the Gulf were indicated by the tag recovery data. Southerly movements of Atlantic lobsters into deeper waters (>30 m) offshore from the reef may have occurred, but were undetected because the swift currents of the Gulf Stream prevented the deployment of fishing gear.

These observed movements of spiny lobsters in the lower Florida Keys may be related to multiple phenomena associated with the life history of the spiny lobster. Gulf lobsters, many of which were smaller in size than their Atlantic counterparts, may have been immigrating from Florida Bay, an important nursery area for the spiny lobster in south Florida (Davis and Dodrill 1981). Also, the larger-sized Gulf lobsters may have originated in the deeper Gulf waters. Inasmuch as most of the tags were recovered during the late summer – autumn (August–October), the apparent movements of Gulf lobsters may have been caused by the occurrence of the fall and winter cold fronts, which begin to move through the area during the latter part of September and October. Similar large-scale autumnal movements of lobsters from shallow areas exposed to winter storms have been reported for the Bahamas (Kanciruk and Herrnkind 1978) and Cuba (Buesa Mas 1970). In the Atlantic, apparent movements of lobsters may be due to the seasonal shifts of adult lobsters from the shallows to the reef for reproduction — after which they return to the shallow onshore waters (Sutcliffe 1952; Davis 1977; Gregory et al. 1982).

No single tagging study can possibly elucidate all aspects of the migratory habits of the spiny lobster. Further studies are required to determine the existence of seasonal differences in movement patterns, the occurrence of movements into the deeper and currently inaccessible fishing areas south of the reef as well as movements further to the west, past the Dry Tortugas, and the potential occurrence of movements from the deeper waters of the Gulf of Mexico into the waters of the lower Keys.

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## References

ANONYMOUS. 1982. Fishery management plan, environmental impact statement and regulatory impact review for spiny lobster in the Gulf of Mexico and South Atlantic. Available from the Gulf of Mexico Fishery Management Council, 5401 West Kennedy Boulevard, Lincoln Center, Suite 881, Tampa, FL 33609.

BATSCHELET, E. 1981. Circular statistics in biology. Academic Press, New York, NY.

BUESA MAS, R. J. 1970. Migrations of the lobster *Panulirus argus*. Mar y Pesca 60: 22–27. (Trans. from Spanish by P. Aukland, National Marine Fisheries Service. Foreign Fish. Trans. 11403)

CRAWFORD, D. R., AND W. J. J. DE SMIDT. 1922. The spiny lobster, *Panulirus argus* of southern Florida: its natural history and utilization. Bull. U.S. Bur. Fish. 38(925): 281–310.

CUSHING, D. H. 1968. Fisheries biology: a study in population dynamics. University of Wisconsin Press, Madison, WI.

DAVIS, G. E. 1977. Effects of recreational harvest on a spiny lobster, *Panulirus argus*, population. Bull. Mar. Sci. 27: 223–236.

1978. Field evaluation of a tag for juvenile spiny lobsters, *Panulirus argus*. Trans. Am. Fish. Soc. 107: 100–103.

DAVIS, G. E., AND J. W. DODRILL. 1981. Marine parks and sanctuaries for spiny lobster fisheries management. Proc. Gulf Caribb. Fish. Inst. 32: 194–207.

DAWSON, C. E., AND C. P. IDYLL. 1951. Investigations on the Florida spiny lobster, *Panulirus argus* (Latreille). Fla. State Board Conserv. Tech. Ser. 2: 39 p.

GREGORY, D. R. JR., R. F. LABISKY, AND C. L. COMBS. 1982. Reproductive dynamics of the spiny lobster *Panulirus argus* in south Florida. Trans. Am. Fish. Soc. 111: 575–584.

HARDEN JONES, F. R. 1968. Fish migration. Edward Arnold, London, England.

HERRNKIND, W. F. 1980. Spiny lobsters: patterns of movement, p. 349–407. *In* S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1: Physiology and behavior. Academic Press, New York, NY.

JONES, R. 1976. The use of marking data in fish population analysis. FAO Fish. Tech. Paper 153: 1–42.

KANCIRUK, P., AND W. HERRNKIND. 1978. Mass migration of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): behavior and environmental correlates. Bull. Mar. Sci. 28: 601–623.

LABISKY, R. F., D. R. GREGORY, JR., AND J. A. CONTI. 1980. Florida's spiny lobster fishery: an historical perspective. Fisheries 5: 28–37.

LYONS, W. G., D. G. BARBER, S. M. FOSTER, F. S. KENNEDY, JR., AND G. R. MILANO. 1981. The spiny lobster, *Panulirus argus*, in the middle and upper Florida Keys: population structure, seasonal dynamics, and reproduction. Fla. Mar. Res. Publ. 38: 1–38.

MARDIA, K. V., AND B. D. SPURR. 1973. Multisample tests for multimodal and axial circular populations. J. R. Stat. Soc. (Ser. B) 35: 422–436.

SAILA, S. B. 1961. A study of winter flounder movements. Limnol. Oceanogr. 6: 292–298.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, NY.

SUTCLIFFE, W. H. JR. 1952. Some observations of the breeding and migration of the Bermuda spiny lobster, *Panulirus argus*. Proc. Gulf Caribb. Fish. Inst. 4: 64–68.

WARNER, R. E., C. L. COMBS, AND D. R. GREGORY, JR. 1977. Biological studies of the spiny lobster, *Panulirus argus* (Decapoda: Palinuridae), in south Florida. Proc. Gulf Caribb. Fish. Inst. 29: 166–183.

# Session 5
# Recruitment Enhancement

Chairman: G. Y. Conan

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# Conservation of Recruitment of the Western Rock Lobster (*Panulirus cygnus*) by Improving Survival and Growth of Undersize Rock Lobsters Captured and Returned by Fishermen to the Sea

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Brown, R. S., and N. Caputi. 1986. Conservation of recruitment of the western rock lobster (*Panulirus cygnus*) by improving survival and growth of undersize rock lobsters captured and returned by fishermen to the sea. Can. J. Fish. Aquat. Sci. 43: 2236–2242.

The western rock lobster (*Panulirus cygnus*) fishery is one of the largest rock lobster fisheries in the world with an average catch (1974–75 to 1983–84) of 10 million kg. On average, 18 million undersize rock lobsters (sublegal size) are caught, handled, and returned to the sea each season despite the release of many through mandatory escape gaps in traps. Depending on the handling procedure, undersize rock lobsters experience various degrees of exposure, displacement, and damage which adversely affect their survival and growth. Laboratory, field, and tagging experiments showed that handling produced a mortality of 14.6% that costs the industry in excess of $A13 million per season (1984–85 values). An education programme has resulted in improved handling of undersize rock lobsters, and trials have shown that by increasing the size of the escape gap, the number of undersize rock lobsters handled can be reduced by 40–60%. This would result in a significant enhancement of recruitment to the fishery.

La langouste *Panulirus cygnus* fait l'objet de l'une des pêcheries de langoustes les plus importantes du monde avec des prises moyennes de 10 millions de kilogrammes entre 1974–1975 et 1983–1984. En moyenne, 18 millions de langoustes de taille inférieure à la taille légale sont chaque saison capturées, manipulées et remises à l'eau bien que les casiers soient obligatoirement dotés d'orifices permettant à un grand nombre de ces crustacés de s'échapper. Selon la méthode de manutention, les petites langoustes souffrent à des degrés divers d'être sorties de l'eau, déplacées et blessées, ce qui a un effet négatif sur leur survie et leur croissance. Des expériences menées en laboratoire et sur le terrain et des opérations de marquage ont montré que la manutention cause une mortalité de 14,6 % qui coûte à l'industrie plus de 13 millions de dollars par saison (chiffres de 1984–1985). Un programme d'éducation a permis d'améliorer la manutention des petites langoustes, et des essais ont montré qu'en augmentant la taille de l'orifice d'échappement, on peut réduire de 40 à 60 % le nombre de petites langoustes manipulées, ce qui permettrait d'augmenter notablement le recrutement pour la pêche.

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The western rock lobster *Panulirus cygnus* has been exploited commercially in Western Australia since before 1897, when the first regulation, a minimum size, was proclaimed. Rock lobsters were lightly exploited in the 1930's when 250 000 kg was caught for the local market. The fishery developed into an export one producing 1 million kg in 1948 and now produces an average of 10 million $kg \cdot yr^{-1}$ (10-yr average, 1974–75 to 1983–84) worth over $A130 million to fishermen in 1985.

The main thrust of management measures has been to contain expansion in fishing effort to maintain stability of the stock (Bowen 1971, 1980; Hancock 1981; Morgan and Barker 1982). The industry has been operating under a limited entry regime since 1963 (Morgan and Barker 1982), and 765 boats are currently licensed to operate 76 000 pots (traps). The four main regulations that govern the fishery (Bowen 1980; Hancock 1981) are as follows: (a) a minimum legal size of 76 mm carapace length, which is close to the size at first maturity (Morgan 1972); (b) berried females must be returned to the sea; (c) closed season 1 July – 14 November for coastal areas and 1 July – 14 March for Abrolhos Is area; (d) all pots must be fitted with a 54 × 305 mm gap to reduce the retention of undersize rock lobsters (Bowen 1963).

With an annual rate of exploitation of 0.60 and an overall rate of exploitation of 0.85 (N. G. Hall, P.O. Box 20, North Beach, Western Australia 6020, unpubl. data) the fishery depends largely on new recruits. It is important to ensure that the millions of undersize rock lobsters, which despite the use of escape gaps are caught and handled each season, are conserved so that the maximum recruitment occurs. Research on lobster fisheries has found escape gaps to be an effective way of reducing the capture of undersize rock lobsters (e.g. Bowen 1963; Krouse and Thomas 1975; Krouse 1978; Fogarty and Borden 1980; Harris 1980; Anonymous 1983, Skillman et al. 1984).

This paper reviews research conducted in Western Australia

TABLE 1. Percentage of undersize rock lobsters sorted and extent of exposure for each sorting technique for the (A) initial study and (B) follow-up study.

| Sorting technique[a] | % undersize rock lobsters sorted | Exposure times (min) 0–10 | 10–20 | 20–30 | 30–40 | >40 |
|---|---|---|---|---|---|---|
| *A. Initial study (1977–80)* | | | | | | |
| Direct from pot | 6.4 | 100 | | | | |
| After each pot | 13.0 | 100 | —[b] | | | |
| Continuous | 26.2 | 93.5 | 5.0 | 1.5 | —[b] | |
| Erratic | 4.5 | 79.0 | 17.0 | 3.5 | 0.5 | |
| At end of line of pots | 40.9 | 59.5 | 21.5 | 10.5 | 4.0 | 4.0 |
| After relaying pots | 9.0 | 45.0 | 19.5 | 16.0 | 9.5 | 10.0 |
| All boats and sorting techniques combined | 100 | 76.0 | 12.0 | 6.5 | 3.0 | 2.5 |
| *B. Follow-up study (1983–84)* | | | | | | |
| Direct from pot | 7.8 | 99.5 | 0.5 | | | |
| After each pot | 40.4 | 98.0 | 1.0 | 0.5 | 0.5 | |
| Continuous | 43.5 | 92.5 | 5.0 | 1.5 | 1.0 | 0.5 |
| Erratic | 4.5 | 66.5 | 27.5 | 2.0 | 1.5 | 3.0 |
| At end of line of pots | 3.9 | 70.0 | 25.0 | 5.0 | —[b] | |
| After relaying pots | 0 | | | | | |
| All boats and sorting techniques combined | 100 | 92.5 | 5.5 | 1.0 | 0.5 | 0.5 |

[a]See methods for complete details of sorting methods.
[b]Less than 0.25.

on fishery-induced mortality of undersize rock lobsters. The major aims of the research were to (a) quantify the magnitude of the problem by determining the handling procedures, the number of undersize rock lobsters captured in a season, and the cost to the industry of any mortality incurred (Brown et al. 1987); (b) examine the effect of factors such as exposure, displacement, and damage on survival and growth (Brown and Caputi 1983, 1985; Brown et al. 1987); and (c) examine the practical ways of reducing this serious source of industry-created wastage through an education programme to improve the methods of handling undersize rock lobsters (Brown et al. 1987; Brown and Dibden 1987). Also presented is information on testing various sizes of escape gap which may reduce further the capture of undersize rock lobsters.

## The Fishery

### Number of Undersize Rock Lobsters Handled

The number of undersize rock lobsters handled each season by rock lobster fishermen was estimated in two ways (Brown et al. 1987). The first involved obtaining the number of undersize rock lobsters caught per pot lift for four depths at four locations during each month and then raised to the total number of potlifts. The second method consisted of weighting up the ratio of the number of undersize to legal-size rock lobsters caught to the total catch.

These estimates were made from seasons of low, average, and high abundance and ranged between 15.1 and 19.6 million undersize rock lobsters. Eighteen million was used as the basis of all further calculations throughout this paper (Brown et al. 1987).

### Undersize Rock Lobster Handling Procedures

The monitoring of 125 boats from seven locations for 1 d each (15% of the total fleet) between 1977–78 and 1979–80 (Brown et al. 1987) identified six handling methods that were used by commercial fishermen when sorting the undersize from the legal-size rock lobsters: (1) sorting direct from the pot — rock lobsters were measured and undersize ones were returned to the sea immediately; (2) sorting after each pot — all rock lobsters were transferred to a sorting box and were then sorted before the next pot was pulled; (3) continuous sorting — no specific time was allocated to sorting, which was performed when possible; during periods of high catch or poor weather, lobsters tended to accumulate leading to longer exposures; (4) erratic sorting — no pattern of sorting was observed; (5) end of line sorting — rock lobsters were not sorted until a line of pots (usually 20–40) had been pulled, rebaited, and stacked; (6) sorting after relaying a line of pots — rock lobsters were not sorted until a line of pots had been pulled, rebaited, and reset, often in a new locality.

The same monitoring procedure for 123 boats was used during the 1983–84 study (Brown and Dibden 1987) to evaluate the success of an education campaign initiated to improve handling procedures based on the results of our previous studies. Table 1 gives the percentage of undersize rock lobsters handled and the percentage of undersize rock lobsters by exposure category for each of the six sorting methods in the initial study and the follow-up study.

## Laboratory Experiments

### Exposure

Five hundred and twenty-four undersize (72–76 mm carapace length (CL)) rock lobsters were exposed to the air for between 0 and 420 min under various conditions of temperature and sunlight (Table 2). Subsequent deaths over a 2-wk period were analysed using a linear logit model (Brown and Caputi

TABLE 2. Laboratory experiments showing the exposure times producing 25 and 50% mortality of undersize rock lobsters exposed to either direct sunlight or shade, at a variety of temperatures. Equations from which the above values were derived were obtained by linear logit analysis.

| Sunlight | Temperature (°C) | Period of exposure (min) producing 25% mortality | Period of exposure (min) producing 50% mortality |
|---|---|---|---|
| Direct | 31–35 | 75 | 100 |
| Direct | 28–28.5 | 130 | 160 |
| Direct | <27 | 210 | 235 |
| Shade | 26.5–32 | 275 | 395 |

1983). The exposure times producing 25 and 50% mortality for the four experiments indicated that mortality increased when animals were exposed in direct sunlight compared with shade and with increasing temperature and period of exposure (Table 2).

### Growth

Two groups of 60 undersize (72–75 mm CL) rock lobsters were maintained until each animal had undergone two moults in order to determine the normal moult increment and intermoult period. Animals in group 1 were then exposed for 0, 15, 30, or 60 min at 34–35°C and those in group 2 for 0, 15, 30, 60 or 120 min at 20–21°C. They were then maintained under the same conditions for at least two further moults to obtain the postexposure moult increment and intermoult period (Brown and Caputi 1985).

Analysis of variance (ANOVA) on growth increments of group 1 animals at the first moult after exposure showed a significant ($P < 0.01$) reduction after other factors were taken into account. However, the effect of exposure on the second moult after exposure was not significant ($P > 0.05$) although this may be due to the small number surviving. The time between the moult prior to exposure and the first moult after exposure (intermoult period) was not significantly affected by exposure, nor was it significant for the following intermoult period. Exposure had a significant effect on the growth increment of group 2 for both the first ($P < 0.001$) and second ($P < 0.01$) moults after exposure. The intermoult period between the moult prior to exposure and the one directly after was not significantly affected ($P > 0.05$), but the following intermoult period was significantly different due mainly to the low number of days between moults for undersize rock lobsters in the 120-min exposure category. In general, the intermoult period did not appear to be affected by exposure.

### Octopus Predation

Ten groups each comprising five undersize rock lobsters exposed to air and five unexposed were placed in a large outdoor aquarium. Undersize rock lobsters were exposed to air for 15 min in three experiments and for 30 min in seven experiments (Brown and Caputi 1983). Three to 5.5 h later, an octopus, which had not been fed for at least 5 d, was introduced for a period of 12 h.

The octopus attacked and killed one exposed lobster in each of the seven experiments involving 30 min of exposure and in one of the three involving 15 min of exposure. In addition, five undersize rock lobsters exposed for 30 min were attacked and damaged (lost appendages). None of the unexposed animals were killed or damaged. No difference was observed between the behaviour of exposed and unexposed undersize rock lobsters by the time the octopus was put in the tank.

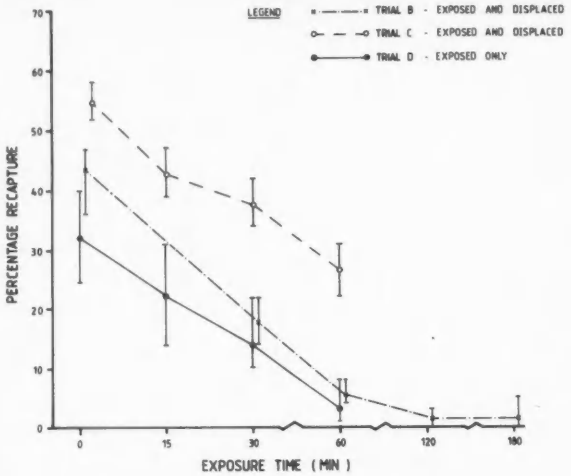


FIG. 1. Percentage of tagged rock lobsters recaptured from the various exposure categories in trials B, C, and D, with 95% confidence limits. (Redrawn from Brown and Caputi (1983) with permission from Fisheries Research.)

## Field Trials

### Behavioural Experiments

Studies involving 350 undersize rock lobsters were conducted at the Abrolhos Is to determine the effect of exposure on their behaviour, after they were returned to the sea (Brown and Caputi 1983). The typical response of an unexposed rock lobster when returned to the water was for it to swim vigorously to the bottom, assume an alert defensive posture, and then search for shelter. If molested by fish, the lobster would use its antennae to fend them off while backing away, and if the threat intensified it would swim backwards rapidly by flipping its tail. Undersize rock lobsters exposed for more than 30 min floated passively to the bottom when returned to the water and did not assume an alert defensive posture, but after a period they usually recovered sufficiently to search for shelter. The percentage of animals that were active once they reached the bottom and the rate of descent (metres per second) decreased with increasing exposure. None of the undersize rock lobsters exposed for less than 30 min but 21 of the 173 (12%) exposed for more than 30 min were predated.

### Tagging Trials

Four tagging trials (Brown and Caputi 1983) were conducted, three at Two Rocks and one at the Abrolhos Is (Fig. 1), to determine the effects of exposure, displacement, and damage on the recapture rate of undersize rock lobsters. Trials were conducted during the two phases of the fishery, the migratory (November–December) and the nonmigratory (January–June).

In trial A, migratory phase, December 1978, the effect of

TABLE 3. Parameters from the linear logit analysis, log of the percent recaptured from the four tagging trials. Significance: $*P < 0.05$; $**P < 0.01$, $***P < 0.001$, NS = not significant, NA = not applicable.

| Factor | Tagging trial | | | |
|---|---|---|---|---|
| | A | B | C | D |
| Size at release | 0.2715*** | 0.2588*** | 0.1907*** | NS |
| Damage | −0.1402*** | −0.2663*** | NS | −0.3297* |
| Exposure | NA | −0.0425*** | −0.0207*** | −0.0405*** |
| Displacement | −0.2454** | NS | −0.2398** | NA |
| Transect | NS | 0.5510*** | 0.2706** | NA |
| Colour | NS | NA | 0.1912* | NA |
| Constant | −0.7840 | −0.7703 | −0.1763 | −0.1128 |
| Goodness of fit ($G^2$) | 63.6 NS | 79.5 NS | 108.7 NS | 15.2 NS |
| Degrees of freedom | 66 | 67 | 98 | 9 |

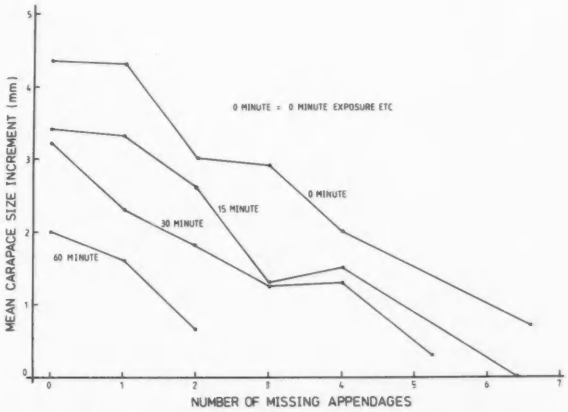


FIG. 2. Mean size increment related to exposure categories and number of missing appendages for rock lobsters recaptured from February 1980 onward in trial C (November–December 1979). Exposure and missing appendage categories with less than five individuals have been combined and are plotted at the mean appendage level. (Redrawn from Brown and Caputi (1985) with permission from Fisheries Bulletin.)

displacement alone was investigated by establishing an experimental grid area on which a baseline of 28 pots, in two parallel lines of 14, were set. Outward from the baseline, five lines of four pots (displacement transects) were set parallel to the baseline at distances of 230, 460, 910, 1370, and 1830 m. Undersize rock lobsters caught in the baseline pots were tagged with western rock lobster tags (Chittleborough 1974a) and released at the various transects along with control animals caught in the pots on that transect. Undersize rock lobsters were kept in circulating seawater tanks with no animal being out of water for more than 3 min. Approximately 2500 undersize rock lobsters were tagged and released.

Similar procedures were followed for trials B (nonmigratory phase, March 1979) and C (migratory phase, December 1979) except that exposures of 0, 15, 30, 60, or 120 min also were combined with displacements up to 3660 m. A fourth trial (D, Abrolhos Is, February 1980) was conducted with exposures of 0, 15, 30, and 60 min with no displacement.

Recaptures from trials A, B, and C were made by commercial fishermen over a number of seasons, while in trial D they were made 1 mo after release by the research vessel.

Table 3 shows the parameters of the significant factors from the linear logit analysis, $\log (p/(1-p))$ of the percent recaptured ($p$) and the goodness of fit parameter ($G^2$), which shows that a good fit was achieved between the expected and actual percent recaptured in the four tagging trials (A, B, C, and D).

In trial A the variation in the proportion of undersize rock lobsters recaptured between the five displacement categories (i.e. those displaced 230, 460, 910, 1370, and 1830 m) was not significant, but the proportion of all the displacement categories combined differed significantly from that of the nondisplaced category (Table 3). Trial C had a similar result for displacement except that significant differences in recapture rate between transects had to be taken into account. Displacement was not significant in trial B conducted during the nonmigratory period. In trials B, C, and D the proportion of undersize rock lobsters recaptured decreased with increasing exposure time (Table 3; Fig. 1). Damage and size at release were generally significant factors in the four trials. Size at release was not significant in trial D, since the recaptures in this trial were made by the research vessel using pots without escape gaps whereas the recaptures from the other trials were made by commercial vessels.

## Growth

For tagging trials A and C conducted in November–December, February was the first month in which there was evidence of moulting (growth), while in trial B (February–March) it was May. Therefore, only recaptures taken after these months have been used in the analysis (see fig. 1 in Brown and Caputi 1985).

An ANOVA on size increment for each of three tagging trials (A, B, and C) was undertaken with the following factors: recapture months, sex, colour, displacement, exposure, size at release, damage, and level of parasite infection (Brown and Caputi 1985). The analysis enables the significance of these factors and covariates to be determined after effects of other factors and covariates are taken into account.

In trial A, the ANOVA resulted in the size increment (CL) per appendage missing being significantly ($P < 0.001$) smaller by 0.48 mm. In trials B and C, the size increment was also significantly ($P < 0.001$) smaller by 0.33 and 0.48 mm per appendage missing, respectively (Fig. 2).

From the ANOVA, size increments of displaced compared with nondisplaced animals were significantly ($P < 0.05$) smaller by 0.32, 0.65, and 0.27 mm for trials A, B, and C, respectively.

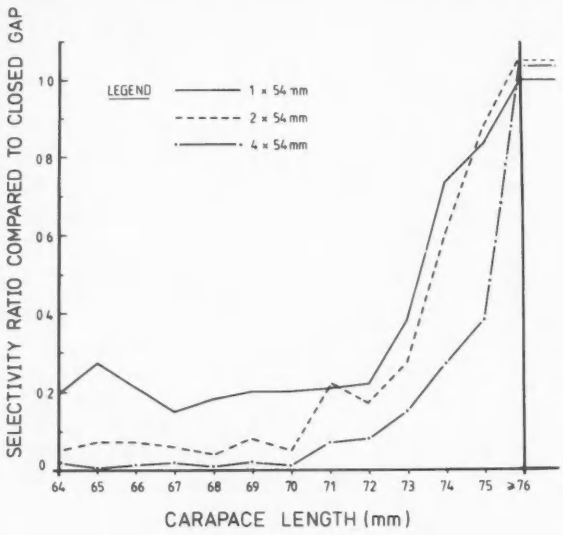


FIG. 3. Escape gap research trial. Selectivity curves for rock lobster in 1-mm size classes for pots with 1 × 54 mm, 2 × 54 mm, and 4 × 54 mm espace gaps relative to pots without an escape gap showing the effect of increasing the number (length) of escape gaps. The selectivity ratio of legal-size rock lobsters has been calculated by combining all animals of 76 mm CL or greater.

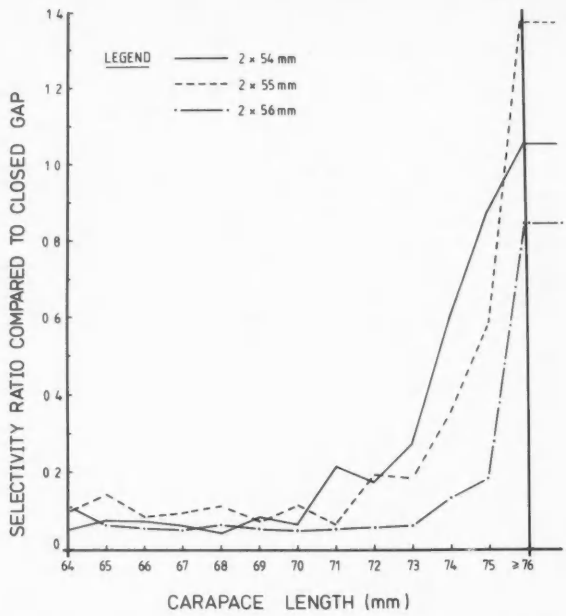


FIG. 4. Escape gap research trial. Selectivity curves for rock lobsters in 1-mm size classes for pots with 2 × 54 mm, 2 × 55 mm, and 2 × 56 mm espace gaps relative to pots without an escape gap showing the affect of increasing the width of the gap. The selectivity ratio of legal-size rock lobsters has been calculated by combining all animals of 76 mm CL or greater.

In trial C, exposure significantly ($P < 0.001$) affected growth with reduced increments of 0.83, 1.34, and 2.30 mm for 15-, 30-, and 60-min exposures, respectively, when compared with the zero exposure category. This also can be seen from Fig. 2, which shows the mean size increment of animals recaptured after February 1980 related to exposure and number of appendages missing. The effect of exposure on growth was not significant for trial B, probably due to the low numbers of exposed animals recaptured after the first moult.

As is usually the case, the size increment was significantly ($P < 0.001$) larger for males than for females in the three trials and there was also a significant ($P < 0.001$) decrease in growth increment with increased carapace size at release and with the level of parasite infection.

## Escape Gap Trials

*Research trial*

A field trial was conducted in November–December 1983 between Dongara and Lancelin to test the efficiency of retaining legal-size and allowing the escape of undersize rock lobsters in pots of 1, 2, and 4 escape gaps of 305 mm length and widths of 54, 55, and 56 mm. A total of 60 batten pots (Morgan and Barker 1974) were used to test the effectiveness of the nine different escape gaps and six pots without escape gaps.

The 60 pots were divided into six groups, with one pot with each type of escape gap in each group. The pots in each of these groups were set randomly along the edge of the reef in a continuous line. Half of the pots, i.e. groups 1, 3, and 5, were pulled each day (24-h soak) for 20 d, while the other pots were pulled every second day (48-h soak). Pots were baited as required with fresh fish and cattle hocks and were shifted to new ground only when all 60 had been pulled.

Figure 3 shows the selectivity curves of 1, 2, and 4 × 54 mm escape gaps for 2-h soak, and Fig. 4 shows the curves for two escape gaps of 54, 55, and 56 mm. The curves are obtained from the ratio of the catch rates of lobsters retained by pots with each gap type compared with pots which had no escape gap (i.e. full retention of all available size classes). The ratio of legal-size animals has been calculated by pooling the values for all lobsters of 76 mm CL or larger.

Generally, as the escape gap increased in both width and number, the percentage of undersize rock lobsters declined but the retention of legal-size rock lobsters was not significantly less. Results for the 48-h soak time were similar but more variable, probably due to smaller sample sizes.

*Commercial trials*

Commercial trials consisted of modifying professional fishermen's pots to incorporate various sizes of escape gap and allowing fishermen to fish them normally. Five fishermen at different locations conducted trials in the 1983–84 season, each using 10 pots, i.e. two pots each with the following escape gap configuration: 1 × 54 mm, 2 × 54 mm, 1 × 55 mm, 2 × 55 mm, and 1 × 56 mm. The pots were set randomly in two groups of five, with one pot of each escape gap type.

Figure 5 shows the ratio of undersize and legal-size rock lobsters retained by various-size escape gaps compared with a 1 × 54 mm gap (currently used) for a 24-h soak period. The ratio of undersize rock lobsters retained decreased with increasing escape gap size, while the retention of legal-size animals remained relatively constant.

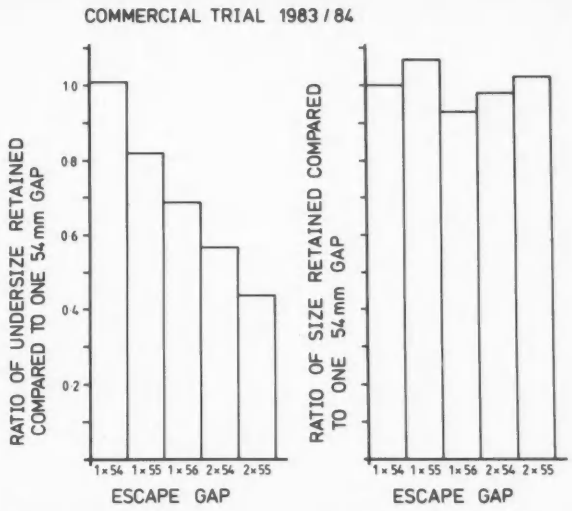


FIG. 5. Escape gap commercial trials. Ratio of undersize and legal-size rock lobsters retained by pots with 1 × 55 mm, 1 × 56 mm, 2 × 54 mm, and 2 × 55 mm escape gaps compared with pots with the current 1 × 54 mm gap.

## General Discussion

The reduction in recapture rates observed during the study can be related directly to mortality of the undersize rock lobsters, with the most likely cause being the debilitating effects of exposure, displacement, and damage making the animals more vulnerable to predation.

### Exposure

In the laboratory and field experiments, exposure decreased survival in direct proportion to the length of exposure (Table 2; Fig. 1). Similar results were obtained by Lyons and Kennedy (1981) for *Panulirus argus*. Octopi that are a major predator of pot-caught rock lobsters (Joll 1977) attacked exposed rather than unexposed undersize rock lobsters even though the exposed animals appeared unaffected after exposures of 15 or 30 min and a recovery period of up to 5.5 h. In the field experiments on behaviour, no undersize rock lobsters exposed for less than 30 min were seen to be predated. However, this may be due to the short time available to observe returned animals.

### Displacement

Undersize rock lobsters in the migratory and newly post-moult phase were most affected by displacement, with the two November–December trials A and C resulting in a reduction in recapture rates of displaced undersize rock lobsters of 14.3 and 16.4%, respectively, compared with recaptures of non-displaced animals. These results agree in general with the observations of Chittleborough (1974b) who found that abnormal patterns of movement and reduced recapture rates resulted from displacement. The fact that the recapture rate did not decrease with increasing distance displaced suggests that any relocation whatsoever outside the animal's home range produces the effect, which presumably makes the lobsters more vulnerable to predation.

### Damage

The extent of damage was related to exposure, and damage significantly reduced the survival of undersize rock lobsters. Increased vulnerability to predation resulting from reduced mobility was the most likely cause of mortality.

### Growth

Exposure of undersize rock lobsters caused a reduction in growth increment at the first moult after exposure in both field and laboratory trials. Damage (Fig. 2) and displacement also had a deterimental effect on growth. These results are similar to those of Davis and Dodril (1980) and Davis (1981) which showed the negative effect of injuries (limb loss) on the growth of *P. argus*. However, their research did not show a proportional relationship between degree of injury and degree of moult increment depression, as was shown for *Hemigrapsus oregensis* and *Pachygrapsus crassipes* (Kuris and Mager 1975) and *P. cygnus*.

As discussed by Davis (1981), reduced growth could result in (1) undersize rock lobsters remaining below legal size for longer and therefore being subject both to additional natural mortality and a greater possibility of multiple capture and handling, (2) affected animals entering the fishery at a smaller size, thereby reducing the harvestable yield, and (3) affected animals reaching maturity at a smaller size and thus being less fecund, maturity being a function of age (Chittleborough 1974c) and fecundity a function of size (Morgan 1972).

### Overall Effect

The combinations of exposure, damage, and displacement on mortality were examined for synergistic effect but it was not found to be significant. Linear combinations of the factors provided good fits (Brown and Caputi 1983).

In general, undersize rock lobsters exposed (15 min or more), displaced, and damaged suffered a significantly greater mortality and reduced growth than unexposed, nondisplaced, and undamaged undersize rock lobsters. The overall mortality of the 18 million undersize rock lobsters estimated to be handled in a season was calculated to be 14.6%. Allowing for natural mortality (Morgan 1977) before the lobsters reached 76 mm CL (legal size), the additional mortality was estimated at 11.4% (see Brown and Caputi 1983). Using the annual exploitation rate for 1978–79 of 0.60 and taking into account the natural mortality and growth at age, the annual loss to the fishery was calculated at over $A13 million by applying the catch equation over the years the animals would have been present in the fishery. This would be equivalent to an average increase in income for each boat of $A17 000 or to having an additional 80 boats in the industry. In addition to these estimated losses resulting from mortality, there would have been losses due to reduced growth. Moreover, the estimates do not take into account any losses which may result from bringing undersize rock lobsters to the surface and returning them immediately to the sea. Even this process causes damage to the undersize rock lobsters which affects their growth and makes them more vulnerable to predation.

### Education Programme

An 18-mo education programme was conducted (1981 and 1982) publicising the effects of poor handling methods on undersize survival. The education programme was followed by

a study in the 1983–84 season to determine if handling procedures had changed significantly (Brown and Dibden 1987) from those documented in the initial study (1978–80). The 1983–84 study showed that approximately 7.5% of the undersize rock lobsters handled by fishermen were exposed for more than 10 min (Table 1B) compared with 24% in the 1978–80 study (Table 1A). The reduction in exposure can be attributed to the changes in sorting procedures from methods involving long exposures, i.e. sorting after a line of pots was pulled and sorting after relaying a line of pots, to methods giving shorter exposures, i.e. sorting directly from the pot and sorting after each pot (see Table 1).

Although some fishermen's attitudes to handling procedures have improved significantly, more than half (52.5%) of the fishermen monitored still did not sort directly from the pot or after each pot, the two recommended sorting techniques that minimise mortality due to handling.

### Escape Gap Testing

The research escape gap trials showed that a significant reduction in the number of undersize rock lobsters (40–60%) can be achieved without a reduction in the catch of legal-sized rock lobsters by increasing the size of the current single 54-mm escape gap. A similar trend is seen in the results of the commercial trials (Fig. 5) where the number of undersize rock lobsters captured was reduced by approximately 40 and 50% for 2 × 54 mm and 2 × 55 mm gaps, respectively, and the catch of size was unaffected. Figures 3 and 4 show that the larger gaps, both in length and width, lower the retention of undersize rock lobsters, especially in the 72–76 mm CL range.

From these results, multiples of 54- or 55-mm gaps appear to offer the best solution for reducing the catch and hence mortality of undersize rock lobsters while reassuring fishermen that their catch of size would be maintained. A further benefit of the more efficient escape gap would be less sorting and therefore faster handling of undersize rock lobsters retained, resulting in reduced exposure.

## Conclusions

(1) The major conclusion is the need to increase the size of the current escape gap. From the above results the most efficient and practical gap to incorporate into pots would be two to four gaps of either 54 or 55 × 305 mm, which could reduce the retention of undersize rock lobsters by 40–60%.

(2) Even with a more efficient escape gap than that currently used, millions of undersize rock lobsters would still be handled each season. Therefore, it is essential these animals are given the shortest possible exposure aboard boat and no displacement. To achieve the maximum survival of handled undersize rock lobsters, fishermen must aim to sort all rock lobsters from one pot before the next pot is hauled. This can be achieved only through further education and publicity.

With the adoption of a more efficient escape gap and further improvement in handling procedures, fishery-induced handling mortality can be reduced significantly with the result of enhanced recruitment to the fishery.

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## References

ANONYMOUS. 1983. Escape gaps proved in west coast trial. FIN TAS, Fish. Ind. News Tasmania. 6(1): 5.

BOWEN, B. K. 1963. Preliminary report on the effectiveness of escape gaps in crayfish pots. Fish. Dep. West. Aust. Rep. II: 13 p.

1971. Management of the western rock lobster (*Panulirus longipes cygnus* George). Proc. Indo-Pac. Fish. Counc. 14(2): 139–153.

1980. Spiny lobster fishery management. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. II. Academic Press, New York, NY. 390 p.

BROWN, R. S., AND N. CAPUTI. 1983. Factors affecting the recapture of undersize western rock lobster *Panulirus cygnus* George returned by fishermen to the sea. Fish. Res. 2: 103–128.

1985. Factors affecting the growth of undersize western rock lobster *Panulirus cygnus* George returned by fishermen to the sea. Fish. Bull. 83(4): 567–574.

BROWN, R. S., N. CAPUTI, J. PRINCE, AND J. JENKE. 1987. The fishery induced mortality of undersize western rock lobster. Fish. Dep. Bull. (In press)

BROWN, R. S., AND C. J. DIBDEN. 1987. A re-examination of the techniques used for handling undersize rock lobsters. Fish. Dep. Rep. (In press)

CHITTLEBOROUGH, R. G. 1974a. Development of a tag for the western rock lobster. CSIRO. Div. Fish. Oceanogr. Rep. 56: 19 p.

1974b. Home range, homing and dominance in juvenile western rock lobsters. Aust. J. Mar. Freshwater Res. 25: 227–234.

1974c. Western rock lobster reared to maturity. Aust. J. Mar. Freshwater Res. 25: 221–225.

DAVIS, G. E. 1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fish. Bull. 78(4): 979–984.

DAVIS, G. E., AND J. W. DODRIL. 1980. Marine parks and sanctuaries for spiny lobster fishery management. Proc. Gulf Caribb. Fish. Inst. 33: 194–207.

FOGARTY, M. J., AND D. V. D. BORDEN. 1980. Effect of trap venting on gear selectivity in the inshore Rhode Island American lobster, *Homarus americanus*, fishery. Fish. Bull. 77(4): 925–933.

HANCOCK, D. A. 1981. Research for management of the rock lobster fishery of Western Australia. Proc. Gulf Caribb. Fish. Inst. 33: 207–229.

HARRIS, K. 1980. Escape gaps in rock lobster pots. Fish. Ind. News Tasmania 2(4): 40–43.

JOLL, L. M. 1977. The predation of pot caught western rock lobster (*Panulirus longipes cygnus*) by octopus. Dep. Fish. Wildl. West. Aust. Rep. 29: 11 p.

KROUSE, J. S. 1978. Effectiveness of escape vent shape in traps for catching legal size lobsters, *Homarus americanus*, and harvestable-sized crabs, *Cancer borealis* and *Cancer irroratus*. Fish. Bull. 76(2): 425–432.

KROUSE, J. S., AND J. C. THOMAS. 1975. Effects of trap selectivity and some population parameters on size composition of the American lobster, *Homarus americanus*, catch along the Maine coast. Fish. Bull. 73(4): 862–871.

KURIS, A. M., AND M. MAGER. 1975. Effect of limb regeneration on size increases at moult of the shore crabs *Hemigrapsus oregonensis* and *Pachygrapsus crassipes*. J. Exp. Zool. 193: 353–359.

LYONS, W. G., AND F. S. KENNEDY. 1981. Effects of harvest techniques on sublegal spiny lobsters and on subsequent fishing yield. Proc. Gulf. Caribb. Fish. Inst. 33: 290–300.

MORGAN, G. R. 1972. Fecundity in the western rock lobster *Panulirus longipes cygnus* (George) (Crustacea:Decapoda:Palinuridae). Aust. J. Mar. Freshwater Res. 23: 133–141.

1977. Aspects of the population dynamics of the western rock lobster and their role in management. Ph.D. thesis, University of Western Australia, c/o P.O. Box 20, North Beach 6020, Western Australia.

MORGAN, G. R., AND E. H. BARKER. 1974. The western rock lobster fishery 1972–1973. Dep. Fish. Wildl. West. Aust. Rep. 15: 22 p.

1982. The western rock lobster fishery 1961–1971. Dep. Fish. Wildl. West. Aust. Rep. 55: 41 p.

SKILLMAN, R. A., A. R. EVERSON, AND G. L. KAMER. 1984. Escape vent experimental procedure for the spiny lobster fishery under management of the Magnus Fisheries Conservation and Management Act. Southwest Fisheries Centre, Admin. Rep. H-84-13.

# Factors Affecting Growth and Maturation of Spiny Lobsters, *Panulirus argus*, in the Florida Keys

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Overall growth rates of sublegal-sized (50–75 mm carapace length (CL)) and large (≥76 mm CL) spiny lobsters, *Panulirus argus*, in the Florida Keys were 0.46 and 0.15 mm CL/wk; growth rates were 48 and 67% less, respectively, in winter than in summer. Injuries caused a significant 39% growth reduction in small (≤60 mm CL) lobsters. Growth decreased dramatically between 74 mm CL (0.46 mm CL/wk) and 76 mm CL (0.23 CL/wk). Between 71–75 and 76–80 mm CL size classes, intermolt periods of females increased 58% and molt increments decreased 16%; male intermolt periods increased 33% but molt increments did not change until 85 mm CL. Consequently, large (≥76 mm CL) males grew 33% faster than females. Changes in growth rates signified a shift in energy use at onset of maturation.

Le taux global de croissance des langoustes *Panulirus argus* de taille inférieure à la taille légale (50–75 mm de longueur de la carapace (LC)) et de grande taille (≥ 76 mm LC) était respectivement, dans les Keys de Floride, de 0,46 et de 0,15 mm par semaine; les taux de croissance étaient respectivement inférieurs de 48 et de 67 % en hiver par rapport à l'été. Les blessures causaient une réduction notable de la croissance (39 %) chez les petites langoustes (≤ 60 mm). La croissance était fortement réduite entre 74 mm (0,46 mm par semaine) et 76 mm (0,23 mm par semaine). Entre les classes de taille 71–75 mm et 76–80 mm, les périodes intermues des femelles augmentaient de 58 % et l'accroissement à la mue diminuait de 16 %; les périodes intermues des mâles augmentaient de 33 % mais l'accroissement à la mue ne changeait pas avant la taille de 85 mm. En conséquence, les gros mâles (≥ 76 mm) présentaient une croissance 33 % plus rapide que celle des femelles. Les changements dans le taux de croissance révélaient une orientation différente dans l'utilisation de l'énergie au début de la maturation.

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Understanding growth is critical to spiny lobster fishery management, especially in making informed decisions concerning optimal minimum legal size. Numerous factors, including maturation (Hancock 1977), temperature (Chittleborough 1975; Davis 1981), injuries (Davis 1981; Brown and Caputi 1985), handling and exposure (Brown and Caputi 1985), and confinement in traps (F. S. Kennedy, Jr., Bureau of Marine Research, 100 Eighth Ave. SE, St. Petersburg, FL, unpubl. data), affect growth of palinurid lobsters. Management measures for the spiny lobster, *Panulirus argus*, fishery of south Florida consist principally of a minimum legal harvest size of 3 in. (76 mm) carapace length (CL) or 5.5 in. (140 mm) tail length and a closed season from April 1 to July 26. Several investigators have proposed that minimum legal size of *P. argus* in Florida be increased to sizes ranging from 79 to 90 mm CL (Dawson and Idyll 1951; Robinson and Dimitriou 1963; Lyons et al. 1981; Gregory et al. 1982) to allow a greater proportion of lobsters to mature prior to harvest. In this paper, several factors affecting growth of commercially fished *P. argus* in Florida are examined, and implications to maturation and fishery yield are discussed.

## Methods

Lobsters were captured in standard slat traps pulled weekly from April 1978 through March 1979 at nine locations in the middle and upper Florida Keys, USA. Sites ranged from shallow, juvenile-dominated areas of Florida Bay to deep Atlantic reef areas occupied principally by larger, mature spiny lobsters. See Lyons et al. (1981) for further descriptions of sites and methods.

At time of capture, lobsters were tagged with Floy No. 68B spaghetti tags placed in the dorsolateral extensor muscle between the cephalothorax and abdomen (Davis 1978). Data collected for each lobster included capture date, sex, injuries (old and new), and CL to the nearest millimetre. Lobsters were released after being tagged, and those recaptured in experimental traps or returned by fishermen were reexamined for the above information.

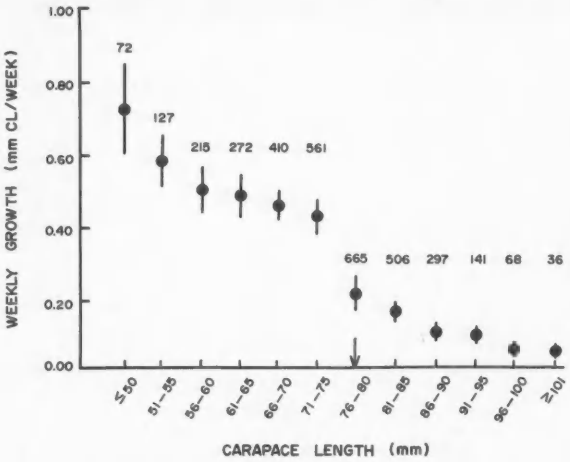


FIG. 1. Mean (±1 SE) weekly growth of all spiny lobsters, *Panulirus argus*, by 5 mm size class. Arrow denotes minimum legal size; *N* values identified for each size class.

Spiny lobsters grow after molting when sizes increase prior to hardening of the new exoskeleton. Growth of individual lobsters was calculated by subtracting initial CL from CL at return. Approximately equal numbers of lobsters showed CL changes of ±1 and ±2 mm, suggesting that measurement error was 2 mm. Consequently, only changes >+2 mm CL were considered to indicate growth. Some lobsters may have molted without growing (Marshall 1948), but these could not be distinguished from those not molting.

Intermolt period was calculated as twice the period required for half of all lobsters to molt (Davis 1981; Waugh 1981; Munro 1983). This assumed that lobsters were distributed randomly throughout the molt cycle, and 50% of the lobsters would have molted when half of the average intermolt period for each size class had elapsed since time of release. Molt increment was calculated only from lobsters at large ≤50% of the average intermolt period for their size group.

To reduce variability inherent in data on discontinuous growth acquired during a tag–recapture study, most analyses were made on growth expressed as rate of CL change per week (Davis 1981); rate per week = CL change per weeks at large for every lobster. Mean weekly growth rate was calculated for each class of observation (e.g. sex, season, injuries). Mean weekly growth rate is a measure which reflects combined effects of molt increment and intermolt period, allowing comparisons over a wide range of sizes and conditions.

Differences between means were evaluated using *t*-tests for unequal sample size (Sokal and Rohlf 1981) for each size class and effector combination. Widely disparate sample sizes and high variability reduced sensitivity of these tests when applied to molt increment.

## Results

Of 19 180 spiny lobsters tagged and released, 3370 (17.5%) were recaptured in experimental traps or returned by fishermen. Recaptured lobsters ranged in size from 35 to 115 mm CL. Relative frequency of returns by 5 mm CL size class is shown in Fig. 1; the modal size class was 76–80 mm CL. Mean growth of sublegal-sized lobsters was 0.46 ± 0.02 mm CL/wk ($N$ = 1657), and mean growth of legal lobsters was 0.15 ± 0.02 mm CL/wk ($N$ = 1713).

Growth rate decreased as size increased (Fig. 1). However, linear regression failed to describe adequately change in growth rate throughout the entire size range, accounting for only 3% of variability. A dramatic decrease in growth rate occurred between the 71–75 and 76–80 mm CL size classes. Mean growth rate by 1 mm size classes revealed that the decrease was sudden and occurred among lobsters between 74 mm CL (0.46 mm/wk) and 76 mm CL (0.23 mm/wk). The change in average growth rate resulted from little change in molt increment but a large shift, from 11.7 to 17.7 wk, in intermolt period (Fig. 2).

Growth rates of sublegal-sized males and females were similar. However, growth of legal-sized females was 33.3% less than that of males (Table 1; Fig. 3). Reduced growth of females was caused by longer intermolt periods and smaller molt increments. Intermolt periods of females increased from 12 to 19 wk, and those of males increased from 12 to 16 wk. Data combined from both sexes indicate that molt increments did not begin to decrease until lobsters attained 86–90 mm CL (Fig. 2). However, average molt increments of females decreased 16% between 71–75 mm CL (6.28 ± 0.47) and 76–80 mm CL (5.29 ± 0.13), whereas those for males remained at approximately 7 mm until 86–90 mm CL (6.30 ± 0.43).

Season affected growth of lobsters, regardless of size (Table 1). The decrease in growth rate between summer (May–October) and winter (November–April) likely was related to the 5.2°C difference in average water temperature (28.3 vs. 23.1°C), although shorter photoperiod in winter also may have been a factor (Chittleborough 1975; Aiken and Waddy 1976). Intermolt period was about 50% longer in winter for both size groups. Molt increment of legal-sized lobsters decreased significantly (30.8%) during winter, whereas the difference for sublegal-sized lobsters was not significant. Seasonal effects were evident in all size classes but were less pronounced in lobsters >90 mm CL, which had small molt increments and molted only 1.7 times per year (Fig. 2).

The influence of injuries on growth was examined for three size classes: ≤60, 61–75, and ≥76 mm CL. Injuries caused a 39% reduction in growth of small (≤60 mm CL) lobsters (Table 1). Intermolt period of small injured lobsters was 1.3 wk longer than that of uninjured lobsters. Injuries did not affect growth in the two larger size groups.

## Discussion

Mean growth rates of juvenile *P. argus* throughout the Caribbean range from 0.41 to 0.65 mm CL/wk (Davis 1981; Lipcius and Herrnkind 1982). Mean growth of sublegal lobsters in this study (0.46 mm CL/wk; 23.9 mm CL/yr) is near the low end of the range. Other studies of juvenile lobsters from south Florida also report growth rates at the low end of this range (Dawson and Idyll 1951; Davis and Dodrill 1980; Davis 1981). A slightly more temperate environment, especially longer and cooler winters, may slow growth of spiny lobsters in Florida.

Injuries are known to reduce growth rates of spiny lobsters (Chittleborough 1975; Davis 1981; Waugh 1981; Brown and Caputi 1985). Loss of limbs may shorten (Chittleborough

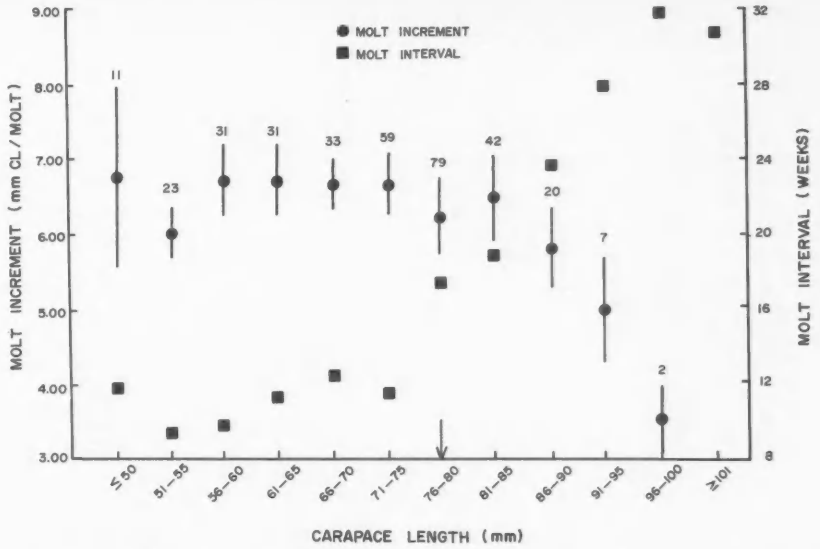


FIG. 2. Mean (±1 SE) molt increment and mean intermolt period for *Panulirus argus* by 5 mm size class. Molt increment calculated for individuals whose time at large was ≤6 wk (size classes <76 mm CL) and ≤10 wk (size classes ≥76 mm CL).

TABLE 1. Effects of sex, season, and injury on growth rate, intermolt period, and molt increment of *Panulirus argus* from the middle and upper Florida Keys. Lobsters are divided into size ranges at minimum legal size and, for injuries, on likelihood of being used as attractants in traps. $t$ = Student's $t$ statistic. * $p < 0.05$; ** $p < 0.01$; ns = not significant.

| Size (mm CL) | | Growth rate (mm CL/wk) | | Intermolt Period (wk) | Molt increment (mm CL) | |
|---|---|---|---|---|---|---|
| | | *N* | Mean ± SE | | *N* | Mean ± SE |
| | | | *Sex* | | | |
| <76 | Males | 699 | 0.50 ± 0.04 | 10.6 | 92 | 6.66 ± 0.24 |
| | Females | 958 | 0.44 ± 0.04 | 13.1 | 96 | 6.56 ± 0.28 |
| | | | $t$ = 1.18 ns | | | $t$ = 0.26 ns |
| ≥76 | Males | 897 | 0.18 ± 0.02 | 17.7 | 93 | 6.57 ± 0.36 |
| | Females | 816 | 0.12 ± 0.03 | 21.4 | 58 | 5.46 ± 0.43 |
| | | | $t$ = 1.91* | | | $t$ = 1.98* |
| | | | *Season* | | | |
| <76 | Summer | 1253 | 0.52 ± 0.03 | 10.9 | 160 | 6.71 ± 0.20 |
| | Winter | 404 | 0.27 ± 0.04 | 16.6 | 28 | 6.00 ± 0.53 |
| | | | $t$ = 5.35** | | | $t$ = 1.26 ns |
| ≥76 | Summer | 1286 | 0.18 ± 0.02 | 18.3 | 129 | 6.43 ± 0.31 |
| | Winter | 427 | 0.06 ± 0.01 | 28.0 | 22 | 4.45 ± 0.35 |
| | | | $t$ = 5.36** | | | $t$ = 4.20** |
| | | | *Injury* | | | |
| ≤60 | Injured | 65 | 0.36 ± 0.06 | 11.0 | 4 | 6.00 ± 0.71 |
| | Uninjured | 349 | 0.59 ± 0.05 | 9.7 | 61 | 6.46 ± 0.33 |
| | | | $t$ = 2.85** | | | $t$ = 0.56 ns |
| 61–75 | Injured | 255 | 0.48 ± 0.06 | 11.2 | 34 | 6.42 ± 0.45 |
| | Uninjured | 988 | 0.42 ± 0.03 | 11.7 | 89 | 6.79 ± 0.28 |
| | | | $t$ = 0.80 ns | | | $t$ = 1.00 ns |
| ≥76 | Injured | 336 | 0.11 ± 0.02 | 20.0 | 22 | 5.90 ± 0.43 |
| | Uninjured | 1377 | 0.16 ± 0.02 | 20.8 | 129 | 6.18 ± 0.32 |
| | | | $t$ = 1.67 ns | | | $t$ = 0.05 ns |

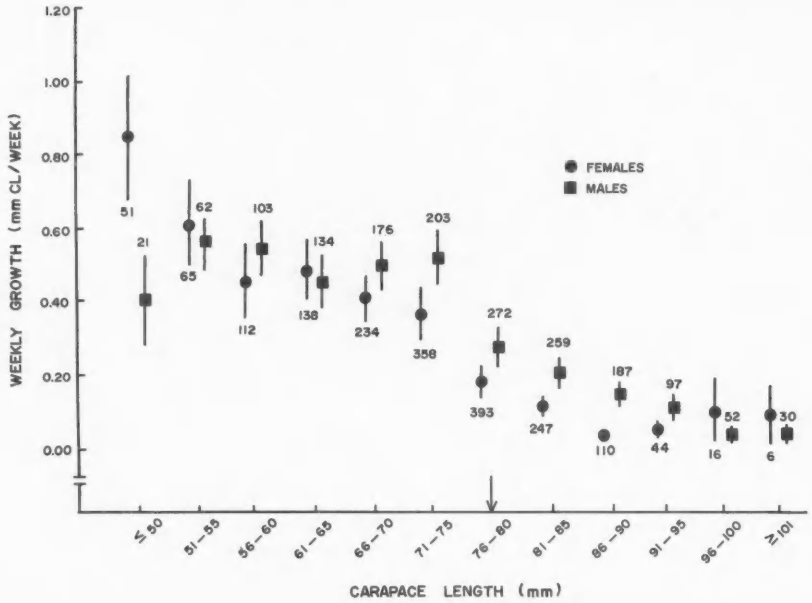


FIG. 3. Mean (±1 SE) weekly growth of male and female *Panulirus argus* by 5 mm size class. Arrow denotes minimum legal size; *N* values identified for each size/sex combination.

1975) or lengthen (Davis 1981) the intermolt period, but smaller molt increments and a net decrease in growth result in either case. Waugh (1981) observed injury-induced growth reduction of 13–51% among juvenile *P. argus* from the Bahamas; differences depended upon gender and season. In the present study, injuries reduced growth only among lobsters ≤60 mm CL. Lobsters of that size are relatively unaffected by the fishery practice of placing sublegal-sized lobsters in traps as attractants (Lyons et al. 1981). The injury-related 39% growth reduction is within the range observed among populations at Biscayne Bay (Davis 1981) and Grand Bahama Island (Waugh 1981), where trap fishing efforts are considerably less.

Injuries did not reduce growth of larger (61–75 mm CL) sublegal-sized lobsters. Regulations permit Florida fishermen to place live sublegal-sized lobsters, predominantly 61–75 mm CL, in traps to serve as attractants, and the fishery is heavily capitalized with more than 600 000 traps and 500 vessels (J. E. Powers, U.S. National Marine Fisheries Service, Southeast Fisheries Center, 75 Virginia Beach Drive, Miami, FL, unpubl. data). As many as 1 million lobsters may be exposed aboard vessels and then confined in traps during the height of the harvest season (Lyons and Kennedy 1981). Many 61–75 mm CL lobsters are confined in traps for extended periods and escape rates are low, 1–3%/d (Davis and Dodrill 1980; Lyons and Kennedy 1981; J. H. Hunt, Bureau of Marine Research, Marathon, FL, unpubl. data). Among lobsters within this size range, the combined effects of air exposure, handling, and confinement may overshadow injury-related reductions in growth evident for smaller *P. argus* less affected by fishery practices.

Air exposure, handling, and confinement of lobsters alter growth processes. Exposure significantly reduced growth of *Panulirus cygnus* tagged and recovered in the Australian fishery (Brown and Caputi 1985). In laboratory trials, growth of *P. cygnus* was reduced for two molts following exposure (Brown and Caputi 1985). Exposed *P. argus* experience a large increase (4.4–49.5 mg/100 mL) in lactic acid concentration and a corresponding drop (7.9–7.4) in blood pH (G. K. Vermeer, Bureau of Marine Research, St. Petersburg, FL, unpubl. data) that may contribute to growth reduction. Brown and Caputi (1983) and Vermeer (unpubl. data) each documented impaired locomotory activity among lobsters following exposure; Vermeer attributed the effect to neural damage which, in some instances, led to lobster deaths. It is reasonable to suspect that such damage would affect foraging capabilities and impair growth of survivors. Lyons and Kennedy (1981) documented weight loss caused by starvation among nonmolting *P. argus* confined in traps. Other experiments testing effects of confinement on tagged lobsters in the south Florida fishery revealed that growth increments of confined lobsters were reduced 28% and intermolt period was twice that of lobsters immediately released (F. S. Kennedy, Jr., Bureau of Marine Research, St. Petersburg, FL, unpubl. data).

Reduction in growth rate among both sexes indicates a change in the focus of energy use from growth to development of gametes and associated secondary sexual characteristics, i.e. onset of maturation. Onset of maturation is that time in the ontogeny of a lobster when processes begin which will culminate in functional reproductive capability. The term does not imply reproductive capability per se, and must not be equated with size at first (i.e. smallest) maturity as expressed by others. Estimation of onset of maturation is derived from measurements taken on the entire population and, as such, represents the mean value for that population. In contrast, size at first maturity documents only the initial, perhaps precocious, appearance of reproductively active individuals and is a poor

estimate of maturation within a population.

The marked change in growth rate indicates that mean size at onset of maturation is near 75 mm CL in the south Florida *P. argus* population. This is supported by studies of other characters (ovigerous setae, spermatophores, eggs) that demonstrate that relatively few *P. argus* are reproductively functional below 85 mm CL in that population (Gregory and Labisky 1981; Lyons et al. 1981; Gregory et al. 1982). However, the size at onset of maturation near 75 mm CL observed here may be reduced from natural size by growth reductions resulting from confinement of 60–75 mm CL lobsters as attractants in traps in the heavily exploited *P. argus* population in south Florida. Size at functional maturity in the Florida Keys population is smaller than in the unfished population at Dry Tortugas nearby (Davis 1975, 1981).

An appropriate minimum legal size, i.e. one that allows a significant portion of the population to reproduce, should be larger than the size at onset of maturation. Minimum sizes that would allow most Florida *P. argus* to reproduce at least once have been estimated variously to occur between 85 and 95 mm CL (Davis 1975; Lyons et al. 1981; Gregory et al. 1982). Increasing minimum legal size to protect spawning stock may affect fishery harvest. Yield per recruit analysis reveals that increasing minimum size to 85 mm CL would increase total harvest from 85 to 95% of maximum yield per recruit (exploitation ratio = 0.90) (Gulf of Mexico and South Atlantic Fishery Management Councils 1982). Thus, increasing minimum size not only will increase spawning potential but likely will increase yield as well.

The marked growth reduction demonstrated here provides the first accurate estimate for population-wide onset of maturation in *P. argus*. Discernment of the size at which growth rate changes requires tagging and recapturing many lobsters. However, application of the method in other Caribbean populations will produce information to evaluate appropriateness of minimum legal sizes and other regulations intended to ensure larval recruitment throughout the range of *P. argus*.

## Acknowledgements

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## References

AIKEN, C. E., AND S. L. WADDY. 1976. Controlling growth and reproduction in the American lobster. Proc. 7th Annu. Meet. World Maricult. Soc.: 415–430.

BROWN, R. S., AND N. CAPUTI. 1983. Factors affecting the recapture of undersize western rock lobster, *Panulirus cygnus* George, returned by fishermen to the sea. Fish. Res. 2: 103–128.

1985. Factors affecting the growth of undersize western rock lobster, *Panulirus cygnus* George, returned by fishermen to the sea. Fish. Bull. (U.S.) 83: 567–574.

CHITTLEBOROUGH, R. G. 1975. Environmental factors affecting growth and survival of juvenile western rock lobsters *Panulirus longipes* (Milne-Edwards). Aust. J. Mar. Freshwater Res. 26: 177–196.

DAVIS, G. E. 1975. Minimum size of mature spiny lobster, *Panulirus argus*, at Dry Tortugas, Florida. Trans. Am. Fish. Soc. 104: 675–676.

1978. Field evaluation of a tag for juvenile spiny lobster, *Panulirus argus*. Trans. Am. Fish. Soc. 107: 100–103.

1981. Effect of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fish. Bull. (U.S.) 78: 979–984.

DAVIS, G. E., AND J. W. DODRILL. 1980. Marine parks and sanctuaries for spiny lobster fishery management. Proc. Gulf Caribb. Fish. Inst. 32: 194–207.

DAWSON, C. E., AND C. P. IDYLL. 1951. Investigations on the Florida spiny lobster, *Panulirus argus* (Latreille). Fla. Board Conserv. Tech. Ser. No. 2: 1–39.

GREGORY, D. R. JR., AND R. F. LABISKY. 1981. Ovigerous setae as an indicator of reproductive maturity in the spiny lobster, *Panulirus argus* (Latreille). Northeast Gulf Sci. 4: 109–113.

GREGORY, D. R. JR., R. F. LABISKY, AND C. L. COMBS. 1982. Reproductive dynamics of the spiny lobster, *Panulirus argus*, in south Florida. Trans. Am. Fish. Soc. 111: 575–584.

GULF OF MEXICO AND SOUTH ATLANTIC FISHERY MANAGEMENT COUNCILS. 1982. Fishery management plan, environmental impact statement and regulatory impact review for spiny lobster in the Gulf of Mexico and south Atlantic. Tampa, FL.

HANCOCK, D. A. 1977. Population ecology and growth, p. 279–286. *In* B. F. Phillips and J. S. Cobb [ed.] Workshop on lobster and rock lobster ecology and physiology. CSIRO Div. Fish. Oceanogr. Circ. 7.

LIPCIUS, R. N., AND W. F. HERRNKIND. 1982. Molt cycle alterations in behavior, feeding and diel rhythms of a decapod crustacean, the spiny lobster, *Panulirus argus*. Mar. Biol. 68: 241–252.

LYONS, W. G., D. G. BARBER, S. M. FOSTER, F. S. KENNEDY, JR., AND G. R. MILANO. 1981. The spiny lobster, *Panulirus argus*, in the middle and upper Florida Keys: population structure, seasonal dynamics and reproduction. Fla. Mar. Res. Publ. 38: 1–38.

LYONS, W. G., AND F. S. KENNEDY, JR. 1981. Effects of harvest techniques on sublegal spiny lobsters and on subsequent fishery yield. Proc. Gulf Caribb. Fish. Inst. 33: 290–300.

MARSHALL, N. 1948. The molting without growth of spiny lobsters, *Panulirus argus*, kept in a live car. Trans. Am. Fish. Soc. 75: 267–269.

MUNRO, J. L. 1983. The biology, ecology and bionomics of spiny lobsters (Palinuridae), spider crabs (Majiidae) and other crustacean resources, p. 206–222. *In* J. L. Munro [ed.] Resources management studies and reviews 7. Manila, Philippines.

ROBINSON, R. K., AND D. DIMITRIOU. 1963. The status of the Florida spiny lobster fishery, 1962–1963. Fla. Board Conserv. Tech. Ser. No. 42: 1–30.

SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman and Co., New York, NY. 852 p.

WAUGH, G. T. 1981. Management of juvenile spiny lobster (*Panulirus argus*) based on estimated biological parameters from Grand Bahama Island, Bahamas. Proc. Gulf Caribb. Fish. Inst. 33: 271–289.

# Session 6
# Ecology of Population Structure

Chairman: J. S. Cobb

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# Competition for Shelter Between Lobsters (*Homarus americanus*) and Jonah Crabs (*Cancer borealis*): Effects of Relative Size

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Richards, R. A., and J. S. Cobb. 1986. Competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*): effects of relative size. Can. J. Fish. Aquat. Sci. 43: 2250–2255.

American lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*) inhabit rocky subtidal areas where they take shelter in crevices or burrows. In previous studies, lobsters dominated crabs of equivalent size in competition for shelter; however, we predicted that large crabs could dominate small lobsters. SCUBA surveys revealed a broad overlap in size of lobsters and Jonah crabs cooccurring in Narragansett Bay, Rhode Island; thus, opportunity exists for interaction between animals disparate in size. In laboratory experiments, relative size did not affect the outcome of competition for shelter: lobsters were competitively superior to crabs of all sizes. However, some crabs excluded lobsters from shelter. Fish predation on lobsters increased significantly when shelter was limited, but predation on crabs did not. Crabs were able to escape predation by rapid burrowing, while lobsters were dependent on locating preexisting refuges. Differential vulnerability to predation may explain the lack of size effect in competition between lobsters and crabs. The cost of not obtaining shelter is lower for crabs than for lobsters; thus, crabs utilize alternatives rather than compete with lobsters.

Le homard américain (*Homarus americanus*) et le crabe nordique (*Cancer borealis*) habitent les zones rocheuses infratidales où ils s'abritent dans des crevasses et des trous. Dans des études précédentes, les homards dominaient les crabes de taille équivalente dans la recherche d'abris, mais nous prédisions que les crabes de grande taille pouvaient dominer les petits homards. Des travaux menés en plongée autonome ont révélé un fort chevauchement des tailles des homards et des crabes nordiques présents dans la baie Narragansett (Rhode Island), et il est donc possible que des interactions se produisent entre des animaux de taille différente. Dans les expériences menées en laboratoire, la taille relative n'affectait pas l'issue de la concurrence pour la recherche d'abris : les homards dominaient les crabes de toutes les tailles. Toutefois, certains crabes parvenaient à chasser les homards des abris. La prédation des poissons sur les homards augmentait fortement quand les abris étaient limités, mais ce n'était pas le cas pour les crabes. Ces derniers pouvaient échapper à la prédation en s'enfouissant rapidement, tandis que les homards étaient tributaires de refuges préalablement repérés. Cette vulnérabilité différente à la prédation peut expliquer l'absence d'effet de la taille dans la concurrence entre les homards et les crabes. Le fait de ne pas trouver d'abri est moins grave pour les crabes que pour les homards, aussi les crabes utilisent-ils d'autres solutions au lieu de rivaliser avec les homards.

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Relative body size can be an important determinant of success in intraspecific and interspecific competition for resources. With few exceptions, larger individuals are able to dominate smaller ones, either of the same species or of another species with similar ecological requirements (see reviews in Morse 1974; Wilson 1975; Connell 1983; Schoener 1983; Werner and Gilliam 1984). Although intraspecific size-dependent interactions have been extensively studied (e.g. Brooke 1981; Keen 1982; Polis 1984), many studies of competition between species consider only interactions between individuals of equivalent size or life history stage. For interacting species in which broad size ranges of individuals utilize similar resources, size-dependent reversals in interspecific dominance relations are possible (e.g. Nilsson 1955; Jenssen 1973; Werner and Gilliam 1984; Rabeni 1985). In such cases, consideration of the size structures of the interacting populations is vital to a thorough understanding of the system.

In Narragansett Bay, Rhode Island, American lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*) are found almost exclusively in rocky subtidal areas (Jeffries 1966; Cobb 1971; Fogarty 1976) where they occupy crevices during diurnal periods of inactivity. Experimental evidence from laboratory and field studies suggests that these species compete for shelter and that lobsters are competitively superior to crabs of equivalent weight (Fogarty 1976; Wang 1982). However, interspecific dominance relations of lobsters and Jonah crabs may depend in part on the relative size of competing individuals. Fogarty (1976) found that competitive outcomes were reversed in laboratory experiments when Jonah crabs were twice the weight of lobsters. Intensive removal of lobsters from subtidal quadrats resulted in increased densities of small (<50 mm carapace width (CW)), but not large (50–150 mm CW), Jonah crabs (Wang 1982).

The competitive dynamics of these species may be important to the lobster fishery. The southern New England inshore lobster fishery removes an estimated 80–84% of the lobsters which attain legal size each year (Anthony 1980), while Jonah crabs are rarely harvested (Briggs and Mushacke 1982). If

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interspecific competition is important in regulating lobster and Jonah crab populations, then intensive fishing of large (legal) lobsters might have allowed Jonah crab populations to increase. This in turn may increase competitive pressure on small (sublegal) lobsters. Thus, the fishery may stress lobster populations both directly, by removing large lobsters, and indirectly, by intensifying competition with Jonah crabs.

The objectives of this study were to (1) document the size composition of lobster and Jonah crab populations cooccurring in Narragansett Bay, (2) examine the degree of overlap in shelter requirements of lobsters and crabs, (3) determine how relative body size influences the outcome of competition for shelter between Jonah crabs and juvenile lobsters, and (4) investigate the effects of competition for shelter on susceptibility to predation of Jonah crabs and juvenile lobsters.

## Methods

### Size Composition of Natural Populations

To determine the size compositions of sympatric lobster and Jonah crab populations, SCUBA divers collected samples at three nearshore locations in Narragansett Bay during August and September of 1983. Locations 1 and 2 were walls of piled rock, inclined at approximately 30°. The rock diameter ranged from 45 to 175 cm at location 1 and from 10 to 45 cm at location 2. Samples were taken at 8–12 m depth. Location 3 was an area of bedrock and sand with scattered boulders and rocks. Samples were taken at a depth of 5–8 m.

Locations were sampled three times, with 4–22 d between successive samples at a site. Collecting began approximately 1 h after sunset, when lobsters and crabs are emerging from shelter. An area roughly 25 × 15 m was sampled by attempting to capture all lobsters and Jonah crabs seen during 1 h, or in one case, until the collection bags were full.

We assumed that the size distribution of animals collected out of their burrows in the early evening was the same as would be obtained by sampling resident animals during the day. To test this assumption, a sample was collected during the day at location 2 for comparison with evening samples from this location. The day sample was taken by SCUBA divers as described above, except that all animals collected had to be removed from burrows.

### Shelter Characteristics

To determine the sizes of lobsters and crabs which were likely to be in direct competition for shelter, the relationship between the size of a shelter and the size of its occupant was examined in field and laboratory studies. Measurements of crabs and their shelters were made in the field by SCUBA divers. After removing a crab from its burrow, divers measured the crab's carapace width (CW, the distance between the two most lateral notches on the carapace), the height and width of the shelter opening, and the length of the shelter. A total of 92 crabs and burrows was measured. Relationships between lobster carapace length (CL) and lobster shelter dimensions were established by Cobb (1971).

Shelter selection experiments were conducted in two 3.7-m-diameter, 0.9-m-deep circular tanks. The tanks were filled to a depth of 0.75 m with running seawater at ambient temperature (12–22°C). In each replicate, lobsters or crabs were presented with three sizes of artificial shelters (rectangular wooden boxes with one open end). Four or five shelters of the predicted size (described below) plus equal numbers of smaller shelters and larger shelters were placed in the tank along with four or five lobsters or crabs of a given size-class. The shelters were arranged in random order with respect to size around the perimeter of the tank, approximately 0.5 m from the edge. Eight centimetres of sand in the bottom of the tanks provided a substratum. Black plastic tank covers were used to decrease the light level and to reduce disturbance caused by activity around the tanks. The number of lobsters or crabs occupying each size of shelter was recorded approximately 24 h after the animals were placed in the tank. A minimum of six replicates (30 animals) were conducted for each species and size-class.

To create a more naturalistic environment, a predatory fish (*Tautoga onitis*) was placed in each pool approximately 15–30 min after the lobsters or crabs were introduced. A cement block with a 20-$cm^3$ opening provided shelter for the fish. A total of six tautogs ranging from 35 to 42 cm total length were used. The fish were fed daily on lobsters and crabs, but were not fed for 3 d prior to use in an experiment.

Lobster and crab size-classes to be used in the experiments were determined by predicting the sizes of animals which would compete for a given size shelter. Shelters were constructed with height equal to half the width and were 30 cm long (after Cobb 1971). Shelter heights ranged from 2.5 to 15.0 cm, in 2.5-cm increments. For each shelter size, lobster size was predicted based on field data relating lobster shelter height to lobster carapace length (Cobb 1971). Shelter height was assumed to be the most important dimension for crabs; thus, crab size was predicted based on body depth, which is closely correlated with CW ($r^2 = 0.99$, Carpenter 1978). The resulting lobster and crab size-classes were as follows:

| | | |
|---|---|---|
| Lobsters | | |
| Small | 36–46 mm CL | 35–80 g |
| Medium | 49–59 mm CL | 100–200 g |
| Crabs | | |
| Small | 65–91 mm CW | 44–145 g |
| Medium | 98–124 mm CW | 141–272 g |
| Large | 132–158 mm CW | 303–404 g |

Animals were always selected according to CL or CW; the estimates of their corresponding weights are included for reference only (lobsters, Aiken 1980; crabs, Carpenter 1978). It was predicted that medium lobsters and small crabs would prefer the same size shelter.

Crabs 65–124 mm CW and all lobsters were obtained by SCUBA diving. Large crabs were donated by a local fish market and probably came from offshore populations. Animals were separated by species and held communally in tanks supplied with running seawater at ambient temperature (12–22°C). Ample shelter and food (fish) were provided. Lobsters and crabs were used within 3 wk of capture and were used only once in an experiment. Changes in aggression over the molt cycle have been documented for lobsters (Tamm and Cobb 1978); thus, only intermolt lobsters were used. It was not possible to precisely determine crab molt stage; however, recently molted crabs and preecdysial females (recognizable by bulges at the epimeral line) were not used.

### Competition for Shelter

In competition experiments, the proportions of lobsters and

crabs obtaining shelter were compared when shelters were abundant or in limited supply. The lobster to crab size ratio was varied to determine how relative size affects the outcome of competition.

The experiments were conducted in a 4.0-m-diameter, 1.4-m-deep circular tank containing approximately 10 cm of sand and filled to a depth of 1.2 m with running seawater at ambient temperature (19–23°C). The tank was covered with a sheet of black plastic. In control treatments, five crabs of a given size-class, five lobsters, and 20 shelters were placed in the tank. In experimental treatments, only five shelters were provided for the same number of lobsters and crabs. The animal densities (0.35 lobsters or crabs $\cdot m^{-2}$) corresponded closely to estimates of natural densities in inshore sand–rock habitats (Cooper et al. 1975; Fogarty 1976; Wang 1982). The shelter size used for each combination of crab and lobster size was based on the results of the shelter selection experiments. Only medium-sized lobsters (49–59 mm CL) were used. Lobsters were matched with the same three size-classes of crabs used in the shelter selection experiments. Two *T. onitis* were added to the tank 30–60 min after the lobsters and crabs had been placed in the tank. A cement shelter as described above was supplied for the fish. After approximately 24 h, the location of the lobsters and crabs in the tank and any mortality were recorded. Ten replicate experiments were conducted, in random order, for each combination of treatment type and crab size-class.

The lobsters and crabs were maintained as described for the shelter selection experiments. Two pairs of *T. onitis* were used alternately on successive days. The fish were not fed in their holding tanks; thus, their only opportunity to feed was during an experiment. The tautogs ranged in size from 34 to 52 cm total length.

## Results

### Size Composition of Natural Populations

Comparison of night and day samples of Jonah crabs from location 2 revealed no difference in size distributions ($p = 0.54$, $G$ test, $G_{50} = 48.2$), thus, night and day samples were combined. Insufficient data were obtained for lobsters in day samples to allow valid comparisons.

Comparison of size frequency distributions of lobsters and Jonah crabs among locations revealed no significant differences for Jonah crabs, but revealed a significant difference in the size distributions of lobsters at locations 1 and 2 ($p < 0.05$, $G$ test, $G_{49} = 74.5$). At location 1, the 64 lobsters captured ranged in size from 12 to 88 mm CL with a median size of 49 mm CL. At location 2, 66 lobsters were captured, ranging in size from 24 to 91 mm CL with a median CL of 45 mm.

The size frequency distributions of lobsters and Jonah crabs obtained in all three locations combined are shown in Fig. 1. Lobsters ranged in size from 12 to 91 mm CL with a median CL of 42 mm. Crabs ranged from 35 to 132 mm CW with a median size of 94 mm CW.

### Shelter Characteristics

Relationships between crab shelter dimensions and crab carapace width derived from field measurements indicated that shelter height and the square root of shelter area were related to crab carpace width ($p < 0.001$, Table 1). However, the fit for both variables was poor ($r^2 = 0.21$). Shelter width and shelter length were not releated to crab carapace width.

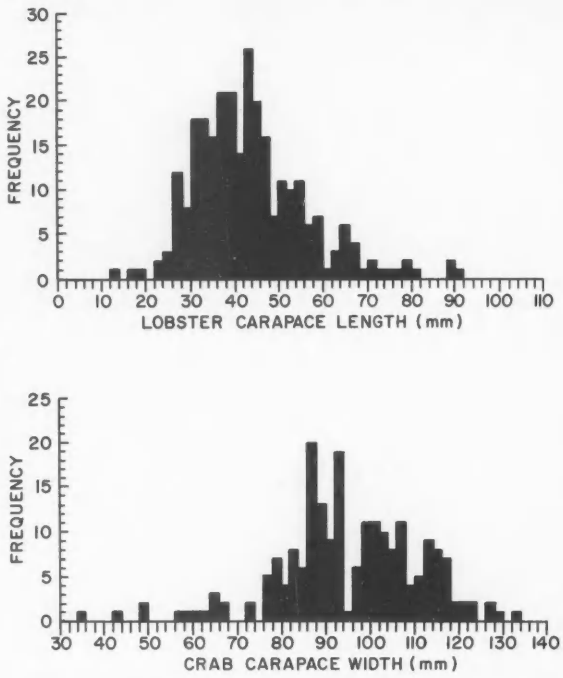


FIG. 1. Size frequency distribution of lobsters obtained in three sampling locations combined.

TABLE 1. Regression models relating ranks of crab carapace width to ranks of crab shelter dimensions. $*p < 0.0001$ that $\beta = 0$; df = total degrees of freedom.

| Shelter dimension | Regression model | df | $F$ | $r^2$ |
|---|---|---|---|---|
| Height | 25.002 + 0.450CW | 89 | 22.72* | 0.21 |
| Width | 32.960 + 0.167CW | 79 | 3.07 | 0.04 |
| Depth | 38.279 + 0.126CW | 86 | 1.43 | 0.02 |
| $(\text{Area})^{1/2}$ | 23.142 + 0.378CW | 78 | 18.55* | 0.19 |

In the laboratory, medium crabs and both size-classes of lobsters selected shelter of particular sizes ($\chi^2$ goodness of fit tests, Table 2). Lobsters tended to choose shelters larger than the predicted size; crabs preferred shelters of the predicted size or a size smaller. All surviving lobsters were found inside shelters or in the tautog's shelter. Approximately 50% of the crabs were found outside shelters, usually partially buried in the sand.

### Competition for Shelter

The proportions of both lobsters and crabs occupying shelter were significantly lower in experimental treatments than in controls ($p < 0.001$, Wilcoxon rank sum tests, Table 3). However, crab size had no effect on shelter occupancy by lobsters in either control or experimental treatments ($p > 0.05$, Kruskal–Wallis tests). In experimental treatments, the proportion of crabs occupying shelter was dependent on crab size ($p < 0.05$, Kruskal–Wallis test), with medium crabs showing the lowest occupancy rate.

TABLE 2. Shelters occupied by lobsters and Jonah crabs in the shelter selection experiments. Three sizes of shelters were offered to each size-class of lobsters or crabs. Predated animals are not included in the totals. $N$ = number of animals tested. Asterisks indicate significance levels of $\chi^2$ goodness of fit tests: $*p < 0.05$, $**p < 0.01$, ns = $p > 0.05$.

| | | Shelter dimensions (height × width) | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | $N$ | 2.5×5.0 cm | 5.0×10.0 cm | 7.5×15.0 cm | 10.0×20.0 cm | 12.5×25.0 cm | 15.0×30.0 cm | Not in shelter | $\chi^2$ |
| Lobster size | | | | | | | | | |
| Small (36–46 mm CL) | 42 | 0 | 12[a] | 20 | — | — | — | 6 | 8.33* |
| Medium (49–59 mm CL) | 40 | — | 2 | 16[a] | 18 | — | — | 4 | 12.66** |
| Crab size | | | | | | | | | |
| Small (65–91 mm CW) | 53 | — | 6 | 11[a] | 5 | — | — | 27 | 2.82 ns |
| Medium (98–124 mm CW) | 44 | — | — | 11 | 5[a] | 2 | — | 26 | 7.00* |
| Large (132–158 mm CW) | 30 | — | — | — | 8 | 8[a] | 1 | 12 | 5.77 ns |

[a]Predicted shelter size.

TABLE 3. Proportions of lobsters and crabs in shelter and sharing shelter in the competition experiments. All lobsters were medium size (49–59 mm CL) and crabs were small (65–91 mm CW), medium (98–124 mm CW), or large (132–158 mm CW). Asterisks refer to significant differences between treatments: $**p < 0.01$, $***p < 0.001$.

| Shelter occupant | Control | Experimental |
|---|---|---|
| Lobsters, competing with: | | |
| small crabs | 0.98 | 0.75*** |
| medium crabs | 0.96 | 0.78*** |
| large crabs | 0.98 | 0.70*** |
| Crabs, competing with lobsters | | |
| Small crabs | 0.74 | 0.36*** |
| Medium crabs | 0.66 | 0.20*** |
| Large crabs | 0.86 | 0.40*** |
| Sharing shelter | | |
| Small crabs | 0.08 | 0.26** |
| Medium crabs | 0 | 0.09** |
| Large crabs | 0 | 0.34** |

Multiple occupancy of shelters was infrequent in controls but increased significantly when shelters were limited ($p < 0.01$, Wilcoxon rank sum test, Table 3). The number of animals cohabiting was not dependent on crab size ($p > 0.05$, Kruskal–Wallis tests). In experimental treatments, 12% of cohabited shelters were shared between lobsters, 18% were shared between crabs, and 70% were shared interspecifically. The only shelter sharing which occurred in the controls was between crabs.

Animals that were not in shelter usually were found underneath a shelter or next to a shelter or the tank wall. Use of these alternative positions by crabs depended on crab size in experimental treatments ($p < 0.05$, Kruskal–Wallis test, Table 4). Small crabs tended to occupy more protected positions (under shelters), while larger crabs were more exposed. The only alternative site used by lobsters was underneath shelters, in burrows which they had excavated. More lobsters were underneath shelters in experimental treatments than in controls ($p < 0.01$, Wilcoxon rank sum test).

## Mortality

Mortality of lobsters and crabs was low in control treatments and did not depend on crab size ($p > 0.05$, Kruskal–Wallis tests, Table 5). When shelters were limited, lobster mortality increased significantly ($p < 0.001$, Wilcoxon rank sum test) but did not vary with crab size ($p > 0.05$, Kruskal–Wallis tests). Crab mortality did not differ between control and experimental treatments.

To ascertain whether tautog feed preferentially on crabs or lobsters, feeding records of tautogs in their holding tanks were examined. The tanks contained a single shelter, but no substratum. When equal numbers of lobsters and crabs (either one or two of each species) were offered, significantly more crabs

TABLE 4. Proportions of lobsters and crabs utilizing alternative sites in the competition experiments. Asterisks refer to significance levels for treatment effects: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$, ns = $p > 0.05$.

| | Control | Experimental |
|---|---|---|
| Lobsters | | |
| Under shelter | 0.01 | 0.09** |
| Next to wall or shelter | 0 | 0 |
| Crabs | | |
| Under shelter | | |
| Small | 0.10 | 0.32* |
| Medium | 0 | 0.10* |
| Large | 0 | 0.06 ns |
| Next to wall or shelter | | |
| Small | 0.04 | 0.26** |
| Medium | 0.22 | 0.66*** |
| Large | 0.10 | 0.44** |

TABLE 5. Proportions of lobsters and crabs killed by tautogs in the competition experiments. All lobsters were medium size (49–59 mm CL) and crabs were small (65–91 mm CW), medium (98–124 mm CW), or large (132–158 mm CW). Asterisks refer to significant differences between treatments: $***p < 0.001$.

| | Control | Experimental |
|---|---|---|
| Lobsters, competing with: | | |
| small crabs | 0 | 0.11*** |
| medium crabs | 0.04 | 0.11*** |
| large crabs | 0 | 0.16*** |
| Crabs, competing with lobsters | | |
| Small crabs | 0.06 | 0.04 |
| Medium crabs | 0.06 | 0.07 |
| Large crabs | 0.04 | 0.04 |

TABLE 6. Numbers and proportions of lobsters and crabs eaten by tautogs in their holding tanks. Asterisks refer to significance of $\chi^2$ goodness of fit tests comparing numbers of lobsters and crabs eaten: ***$p < 0.001$, ns = $p > 0.05$.

| | Total number of animals offered | | Lobsters eaten | | Crabs eaten | | |
|---|---|---|---|---|---|---|---|
| Time period | Lobsters | Crabs | Number | Proportion | Number | Proportion | $\chi^2$ |
| Days 1–21 | 35 | 35 | 2 | 0.06 | 17 | 0.49 | 11.84*** |
| Days 22–44 | 22 | 22 | 14 | 0.64 | 12 | 0.55 | 0.15 ns |
| Days 1–44 | 57 | 57 | 16 | 0.28 | 29 | 0.51 | 10.97*** |

than lobsters were eaten ($p < 0.001$, $\chi^2$ test, Table 6). To determine whether changes in tautog feeding occurred over time, data from the first half of the feeding records were compared with data from the second half. During the initial half, significantly more crabs than lobsters were eaten ($p < 0.001$, $\chi^2$ test). During the second half, equal numbers of lobsters and crabs were consumed. Although more of the lobsters offered were consumed in the second half than the first ($p < 0.001$, binomial proportions test), the proportion of crabs consumed did not change ($p > 0.05$, binomial proportions test). Thus, the fish continued to consume crabs as they added lobsters to their diet.

## Discussion

The ability of Jonah crabs and juvenile lobsters to compete for shelter in our laboratory experiments was not a function of relative size. Lobsters fared equally well whether they were matched with small, medium, or large crabs. These results contrast with observed patterns of interspecific dominance, which generally support the premise that the larger of two competitors is dominant (see Connell 1983; Schoener 1983; Werner and Gilliam 1984). In the case of lobsters and Jonah crabs, other factors are apparently more important than, or interact with, body size.

Small-scale habitat partitioning may provide a partial explanation for these results. Jonah crabs appear to be less specific in their microhabitat requirements than are lobsters. The relationship between crab size and crab shelter dimensions in the field was weaker than that found by Cobb (1971) for lobsters. In laboratory experiments, lobsters were found exclusively inside or underneath shelters, while crabs were found in shelters, under shelters, or buried into the sand next to shelters. Similarly, Jonah crabs appear to use a greater variety of crevice configurations in the field than do lobsters (R. A. Richards, pers. obs.). Thus, more suitable habitat space is available to crabs than to lobsters in a given area of rocky habitat.

Since crabs are relatively flexible in habitat use, occupying alternative sites may be less costly than attempting to evict lobsters from mutually preferred shelter sites. This may explain why we did not observe the reversal in dominance seen by Fogarty (1976) when lobsters were matched with crabs of twice their weight. Fogarty's experimental aquaria contained a single shelter but no substratum. Lobsters occupied the shelter in 96% of the trials when matched with crabs of equal weight, but occupied it in only 10% of the trials when paired with crabs of twice their weight. The presence of sand substratum in the current study provided an opportunity for the crabs to burrow and thus may have eased competitive pressure sufficiently to mask the effects of relative size.

Although body size was unimportant, competition with crabs caused an overall decline in the proportion of lobsters occupying shelter. When shelter was abundant, 97% of the lobsters occupied shelter. When shelter was limited, the proportion of lobsters obtaining shelter declined by 23%. Thus, lobsters were affected by competition with crabs of all sizes used in this study (65–158 mm CW).

Mortality was not related to shelter acquisition in equivalent ways for lobsters and crabs. Predation on both species was low when shelter was abundant, but increased by nearly an order of magnitude for lobsters when shelters were limited. In contrast, crab mortality did not increase in experimental treatments. These differences are not the result of a preference of the predatory fish for lobsters. Field-caught tautog initially consumed significantly more crabs than lobsters, but later consumed equal numbers of both. Only laboratory-conditioned fish were used in the competition experiments, and all treatments were conducted in random order; thus, the effects of any change in the tautogs' behavior should have been minimized. The discrepancy in mortality of lobsters and crabs in the competition experiments must therefore have been related to differences in their behavior.

The most important behavioral difference affecting mortality of lobsters and crabs is probably the greater flexibility in habitat use by crabs. This versatility is based on the burrowing ability of crabs. When approached by a predator, crabs usually tucked their walking legs under their bodies and crouched down. If the fish attacked or approached repeatedly, crabs often dug into the substrate, partially or completely burying themsleves. Because fish typically attacked lobsters' and crabs' walking legs first, these responses made crabs more difficult prey. In contrast, lobsters that were approached or attacked generally backed away from the fish with their bodies elevated and chelae extended toward the fish in a meral spread display (Scrivener 1971). Unless they were able to find a shelter, they were vulnerable despite their aggressive stance. In experimental treatments, shelter availability was low; thus, lobster mortality was high.

Presumably, smaller crabs would be more vulnerable to predation than larger ones. However, mortality was not dependent on crab size. When shelters were limited, crabs used alternative sites differentially according to their size. Smaller crabs burrowed completely under shelters more frequently than larger crabs and more frequently in experimental treatments than in controls. Thus, smaller, more vulnerable crabs used strategies which made them less accessible to the fish. Larger crabs have stronger carapaces; thus, simply burrowing next to a vertical surface may have provided adequate protection.

The extent to which competition affects lobster and crab populations under natural conditions is not certain. Wang (1982) found that densities of small Jonah crabs in a shallow rocky habitat increased after a period of intensive lobster re-

moval. When artificial shelters were added, densities of both lobsters and Jonah crabs increased. Similarly, artificial reefs created to increase carrying capacities for lobsters are colonized rapidly and support natural densities of lobsters (Scarratt 1968; Stewart 1970; Sheehy 1976). These observations suggest that shelter may be limiting in the natural environment.

Shelter sites are not uniformly available in the field; thus, it is difficult to ascertain how abundance of shelters in our laboratory experiments compared with shelter abundance in the natural environment. One indication is provided by field surveys (Fogarty 1976) in which 11.9% of 176 lobster and crab burrows examined contained more than one occupant. In our laboratory experiments, 11.5% of shelters were cohabited when shelters were limited. This suggests that shelter availability was more realistic in experimental treatments with half as many shelters as animals than in control treatments with twice as many shelters as animals.

Only a proportion of the crab population would compete directly with lobsters because some crabs occupy sites not suitable for lobsters. However, since lobsters are more specific than crabs in their habitat requirements, crabs of many sizes would overlap in shelter use with lobsters of a narrow size range. Thus, competition between lobsters and crabs would be expected to affect lobsters more seriously than crabs. This is particularly likely, since lobster survival appears to be more closely tied to acquisition of appropriate shelter than is crab survival.

Ecological competition can be an important structuring force in natural communities (see reviews in Connell 1983; Schoener 1983). The results of this and previous studies suggest that competition for shelter may be a significant factor regulating the abundance of Jonah crabs and juvenile lobsters. If intensive removal of lobsters by fishermen has had the same effect as Wang's (1982) experimental removal of juvenile lobsters, then local density, and eventually population size, of Jonah crabs may have increased. If, as the results of this study indicate, competition from all sizes of Jonah crabs is detrimental to juvenile lobsters, then the development of a market for Jonah crabs could benefit fishermen not only on a short-term, direct income basis, but also indirectly by reducing competitive pressure on juvenile lobsters.

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## References

AIKEN, D. E. 1980. Molting and growth, p. 91–163. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. I. Academic Press, New York, NY.

ANTHONY, V. C. 1980. Review of lobster mortality estimates in the United States. *In* V. C. Anthony and J. F. Caddy [ed.] Proceedings of the Canada–U.S. Workshop on status of assessment science for N.W. Atlantic lobster (*Homarus americanus*) stocks, St. Andrews, N.B., Oct. 24–26, 1978. Can. Tech. Rep. Fish. Aquat. Sci. 932: 186 p.

BRIGGS, P. T., AND R. M. MUSHACKE. 1982. Characteristics of the Jonah crab and rock crab in New York waters. N.Y. Fish Game J. 29: 109–126.

BROOKE, M. DEI. 1981. Size as a factor influencing the ownership of copulation burrows by the ghost crab (*Ocypode ceratophthalmus*). Z. Tierpsychol. 55: 63–78.

CARPENTER, R. K. 1978. Aspects of growth, reproduction, distribution and abundance of the Jonah crab (*Cancer borealis*), Stimpson, in Norfolk Canyon and the adjacent slope. M.S. thesis, Department of Marine Science, University of Virginia, Charlottesville, VA. 69 p.

COBB, J. S. 1971. The shelter-related behavior of the lobster, *Homarus americanus*. Ecology 52: 108–115.

CONNELL, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 122: 661–694.

COOPER, R. A., R. A. CLIFFORD, AND C. D. NEWELL. 1975. Seasonal abundance of the American lobster, *Homarus americanus*, in the Boothbay region of Maine. Trans. Am. Fish. Soc. 104: 669–674.

FOGARTY, M. J. 1976. Competition and resource partitioning in two species of *Cancer* (Crustacea, Brachyura). M.S. thesis, Department of Zoology, University of Rhode Island, Kingston, RI. 94 p.

JEFFRIES, H. P. 1966. Partitioning of the estuarine environment by two species of *Cancer*. Ecology 47: 477–481.

JENSSEN, T. A. 1973. Shift in the structural habitat of *Anolis opalinus* due to congeneric competition. Ecology 54: 863–869.

KEEN, W. H. 1982. Behavioral interactions and body size differences in competition for food among juvenile brown bullhead (*Ictalurus nebulosus*). Can. J. Fish. Aquat. Sci. 39: 316–320.

MORSE, D. H. 1974. Niche breadth as a function of social dominance. Am. Nat. 108: 818–830.

NILSSON, N. A. 1955. Studies on the feeding habitat of trout and char in North Swedish lakes. Rep. Inst. Freshwater Res. Drottingholm 36: 163–225.

POLIS, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? Am. Nat. 123: 541–564.

RABENI, C. F. 1985. Resource partitioning by stream-dwelling crayfish: the influence of body size. Am. Midl. Nat. 113: 20–29.

SCARRATT, D. J. 1968. An artificial reef for lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 25: 2683–2690.

SCHOENER, T. W. 1983. Field experiments on interspecific competition. Am. Nat. 122: 240–285.

SCRIVENER, J. C. E. 1971. Agonistic behavior of the American lobster, *Homarus americanus* (Milne-Edwards). Fish. Res. Board Can. Tech. Rep. 235: 1–128.

SHEEHY, D. J. 1976. Utilization of artificial shelters by the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 33: 1615–1622.

STEWART, L. L. 1970. A contribution to the life history of the lobster, *Homarus americanus* (Milne-Edwards). M.Sc. thesis, Univ. Conn., University of Connecticut, Storrs, CT. 50 p.

TAMM, G. R., AND J. S. COBB. 1978. Behavior and the crustacean molt cycle: changes in aggression of *Homarus americanus*. Science (Wash., DC) 200: 79–81.

WANG, D. 1982. The behavioral ecology of competition among three decapod species, the American lobster, *Homarus americanus*, the Jonah crab, *Cancer borealis*, and the rock crab, *Cancer irroratus* in rocky habitats. Ph.D. thesis, University of Rhode Island, Kingston, RI. 90 p.

WERNER, E. E., AND J. F. GILLIAM. 1984. The ontogenetic niche and species interactions in size-structured populations. Annu. Rev. Ecol. Syst. 15: 393–425.

WILSON, D. S. 1975. The adequacy of body size as a niche difference. Am. Nat. 109: 769–784.

# Session 7
# Factors Affecting Growth and Reproduction

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# Environmental Influence on Recruitment of the American Lobster, *Homarus americanus*: A Perspective

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Heredity determines the biological limits within which an organism can function, and environment determines whether those biological limits will be reached. When they are, biological processes essential to the recruitment cycle begin to fail, and recruitment to subsequent life stages is adversely affected. The American lobster, *Homarus americanus*, experiences a spectrum of environmental forces within its natural range. The most important among these are temperature and disease. These, plus anthropogenic changes, fishing pressure, and several factors with local or short-term impact, can cause stress, which is cumulative and debilitating. These factors combine to influence spawning, egg attachment, incubation success, hatching, larval development, growth, maturity, reproductive capability, and geographic distribution of the animal — major elements of the recruitment cycle.

L'hérédité définit les limites biologiques dans lesquelles un organisme peut fonctionner, et l'environnement détermine si ces limites biologiques vont être atteintes. Quand c'est le cas, les processus biologiques essentiels au cycle de recrutement commencent à faire défaut, et le passage au stade biologique suivant en est affecté. Le homard américain, *Homarus americanus*, subit toute une gamme de forces environnementales dans son milieu naturel. Les plus importantes de ces forces sont la température et la maladie. Ces facteurs, auxquels s'ajoutent les changements d'origine anthropique, la pression de pêche et plusieurs éléments ayant un effet local ou à court terme, peuvent causer du stress qui a un effet cumulatif et affaiblissant. Tous ces facteurs se combinent pour influer sur la fraye, la fixation des oeufs, le succès d'incubation, l'éclosion, le développement des larves, la croissance, la maturité, la capacité de reproduction et la distribution géographique de l'animal — éléments principaux du cycle de recrutement.

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*Homarus americanus* ranges throughout the western North Atlantic from Cape Hatteras north to the Strait of Belle Isle and is abundant in the southern Gulf of St. Lawrence, the nearshore waters southwest of Nova Scotia, and the Gulf of Maine out to the canyons of the continental slope. This is a diverse environment that extends from the intertidal zone to depths of 700 m or more and includes protected as well as exposed locations, pristine oceanic waters as well as areas where sewage sludge and industrial wastes have been dumped for 40 yr, and regions where the annual range in water temperature can be as little as 5°C or as much as 20°C. As a result, environmental forces within the natural range of the animal exert a variety of pressures on survival, growth, and reproduction — the trinity of the recruitment cycle.

The interactions between the biological processes of lobsters and the environmental forces that control them are complex. Environmental forces can act singly or synergistically, and their effects can be covert, producing stress that renders the animal more sensitive to events that would normally be tolerated. In addition, the impact of an environmental event can vary with molt stage, season, social conditions, age, sex, nutrition, and reproductive state. Few of these interactions have been studied in detail, and the information relating to the subject is scattered and fragmented. The purpose of this paper is to put the recruitment of the American lobster into perspective in terms of the environmental forces that affect it.

Recruitment in the broadest sense is the passage from one life stage to the next. In a fisheries context, recruitment usually means survival from some earlier life stage to the minimum legal size for the commercial fishery. In this review we consider the starting point for recruitment to be the germinal epithelium and the recruitment cycle to encompass all subsequent life stages. The information summarized here is organized and presented in that format.

## Oocytes and Ova

### Temperature

Temperature is a major factor in the control of oocyte maturation and the incidence and synchronization of spawning (Fig. 1A). The rate of oocyte growth during the final weeks of ovary maturation varies directly with temperature. If winter temperatures of 2–3°C are extended through the following summer, spawning may not occur at all (S. L. Waddy and D. E. Aiken, unpubl.). If the increase in water temperature above 5°C is delayed in spring, final oocyte maturation and spawning will also be delayed.

At the northern limits of the range, summer temperatures occasionally remain so low that some mature females are unable to spawn. The temperature extremes recorded for Comfort Cove, Newfoundland, are in this category (Ennis 1982b). Squires et al. (1971) found that two arms of the same New-

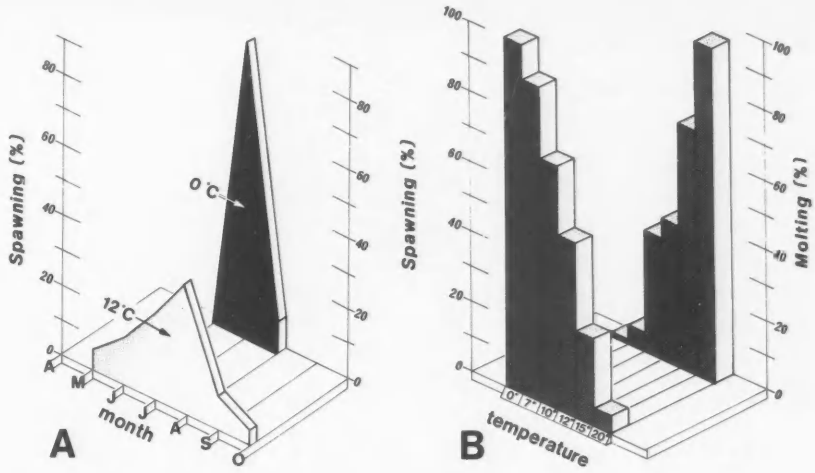


FIG. 1. Influence of temperature on reproduction and molting in mature female American lobsters. (A) Effect of 0 and 12°C winter seawater temperatures on synchrony of spawning during the following summer; (B) effect of various winter seawater temperatures on the relative incidence of molting or spawning during the following summer.

foundland bay had different temperature regimes, and the lobsters in those two bays had different reproductive cycles. In the warmer of the two, lobsters spawned biennially (the normal situation), but in the colder arm, spawning occurred every third year. Similarly, Ennis (1971) found that lobsters in the cold water of the northeast coast of Newfoundland only spawned every fourth or fifth year.

At the southern limit of the range the opposite condition prevails. Winter water temperature must decline to approximately 8–10°C for proper synchronization of molting and reproduction. Above this temperature, molting begins to displace reproduction, and spawning will be spread over a greater portion of the year (Waddy and Aiken 1984b, 1984c, 1984d). This phenomenon also occurs in *H. gammarus* around Jersey in the Channel Islands (S. F. Bossy, pers. comm.). In the summer following a winter of temperatures above 8–10°C the incidence of spawning will decrease and there will be a proportional increase in the incidence of oocyte resorption followed by a molt (Fig. 1B).

Templeman (1940a) was first to note a marked variation in spawning times of lobsters in localities with different temperature regimes (Fig. 2). Inshore areas have greater seasonal temperature changes, and cycles of molting and spawning are more clearly defined. Eighty percent of spawning in some inshore areas occurs within a 3-wk period (Aiken and Waddy 1985c). Offshore, where seasonal temperature changes are more moderate, molting (and possibly spawning, although reproductive cycles of offshore lobsters have not been defined) is spread over a greater proportion of the year (Cooper and Uzmann 1980). This relationship may be modified to some extent by seasonally directed movements of offshore lobsters (Campbell and Stasko 1986).

The environmental factors that control spawning are still under study. Experiments utilizing lobsters from the Gulf of St. Lawrence have indicated that time of spawning is regulated primarily by temperature (Aiken and Waddy 1985a, 1986; Waddy and Aiken 1984a, 1984b, 1984c), but other work has implicated photoperiod (Nelson et al. 1983). The matter is not yet resolved (Aiken and Waddy 1985b; Nelson and Hedgecock 1985; Nelson 1986).

### Stress

Trapping, handling, and confinement in the 2–4 wk prior to spawning can cause the degeneration and resorption of oocytes (Aiken and Waddy 1985c). In areas where lobsters mature at a small size and experience heavy fishing pressure during spring and summer, those that mature below the minimum legal size would be susceptible to oocyte resorption as a result of repeated capture, confinement, and release.

### Other Factors

Reproductive success can also be influenced by lack of food or by deficiencies in dietary lipid or protein which can cause oocyte resorption (Castell and Budson 1974; Castell and Kean 1986). There are also indications that geographic location can influence fecundity, but this is probably an indirect effect (Aiken and Waddy 1980; Campbell and Robinson 1983; Ennis 1981; Squires 1970).

## Embryos

Adverse conditions that are tolerated by the maternal female may quickly kill the embryos she carries. Laboratory studies have shown that environmental conditions influence the security of egg attachment, the success of incubation, the rate of embryonic development, and the survival of embryos (Aiken and Waddy 1985). To survive the 10–12 mo of normal incubation in the wild, an embryo must have sufficient organic reserves, be securely attached to the pleopods, and remain free from disease, predation, and exposure to water of poor quality.

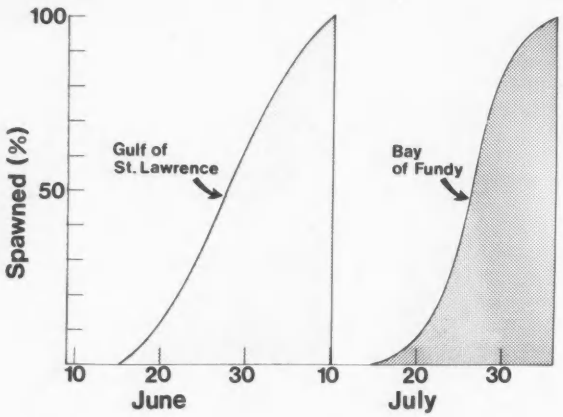


FIG. 2. Influence of temperature on spawning time. Water temperature in the southern Gulf of St. Lawrence may exceed 20°C. In the Bay of Fundy it seldom rises above 12°C (data from Templeman 1940a).

### Temperature

Embryonic development is regulated by temperature (Perkins 1972; Templeman 1940a), and proceeds slowly below 6°C. Hatching can be delayed by as long as 6 mo if the temperature remains at 2–3°C throughout spring, summer, and autumn (Aiken and Waddy 1985c), but will eventually occur, even at that temperature.

Time of onset of hatching varies with year and location. Harding et al. (1982) found that hatching began in St. Georges Bay (southern Gulf of St. Lawrence) when the surface seawater temperature reached 12.5°C, and after a survey of the literature (Harding et al. 1983), concluded that this was a general phenomenon. On the other hand, Fogarty and Lawton (1983) noted that hatching began at a bottom temperature of 8–9°C in the Gulf of Maine, but at 11–13°C further south. Bay of Fundy embryos have consistently started hatching in our laboratory when the water temperature reached 10°C (S. L. Waddy, unpubl.). These variations in temperature at onset of hatching are probably reflections of different temperature histories. These will vary from one ovigerous female to the next according to the time of spawning, differences in local and regional temperatures, and movements of the ovigerous females.

The time required fron onset to completion of hatching of a brood (the hatching period) can extend from a few days to 3 wk or more (Ennis 1975). The duration of the hatching period is determined primarily by the temperature at time of hatching (Herrick 1909; Hughes and Matthiessen 1962; McLeese and Wilder 1964), and in years (or localities) with high summer temperature the hatching period will be shorter than when mean summer temperature is lower (Scarratt 1964).

However, temperature history can alter the normal relationships. The hatching period of embryos held at a constant 20°C will be prolonged, but a brood held 4 or more mo beyond the normal time at 2–3°C will hatch over a brief period when the water is warmed (Aiken 1980). Low temperature therefore synchronizes development of a group of embryos in much the same way it synchronizes the molt cycles of a group of juveniles or adults.

Temperature can also affect lipid conversion efficiency in embryos and, as a result, the quantity of yolk remaining at hatching (Sasaki et al. 1986). These lipid reserves could serve as an important supplemental energy source during the immediate post-hatch period, directly affecting both growth and survival of larvae.

### Stress

The mechanisms that contribute to secure attachment of the spawned eggs to the maternal pleopods are not well understood, but when conditions are not favorable, the eggs will be lost from the pleopods and die. Loss of developing embryos between spawning and hatching has been estimated at 36% for offshore females (Perkins 1971), but embryo loss from relatively undisturbed lobsters in the laboratory is much lower (S. L. Waddy, unpubl.), suggesting that factors in the natural environment aggravate the rate of egg loss.

One factor that can cause significant attrition of embryos is repeated handling and release of ovigerous females during fishing activity. Severe loss of embryos occurs when ovigerous females are taken aboard ship, removed from the trap, and thrown back (S. L. Waddy, unpubl.). The loss may be more pronounced late in development when the embryos are less securely attached, or where fishing is intense.

Loss of embryos can be significant in some localities. Smith (1977) and Ennis and Collins (1983) both found that 14–15% of females were carrying fewer than 150 embryos.

### Disease and Predation

Several microbial epibionts affect lobster embryos (for reviews see Fisher et al. 1978; Sindermann 1977). The filamentous bacterium *Leucothrix* can prolong embryo development by 6 wk or more (Aiken and Waddy 1985c), and severe infections can cause death of the entire brood. Although this bacterium is ubiquitous in the marine environment (Sindermann 1977) and is found on embryos from wild-caught ovigerous lobsters (Johnson et al. 1971; S. L. Waddy, unpubl.), the extent of its effect on natural populations has not been documented. *Leucothrix* is seldom a problem when water quality is good, and its incidence on ovigerous lobsters from the Bay of Fundy varies from none to moderate (S. L. Waddy, unpubl.).

In recent years a nemertean, *Pseudocarcinonemertes homari*, has threatened lobster embryos in Canadian waters (Aiken et al. 1983; 1985; Brattey et al. 1985; Fleming and Gibson 1981; Uhazy et al. 1985; Waddy and Aiken 1985). A similar nemertean, *Carcinonemertes errans*, has caused significant egg loss from Dungeness crabs, *Cancer magister*, off the west coast of the United States (Wickham 1979, 1980, 1986). Laboratory studies showed that *P. homari* had the potential to cause similar problems for *Homarus* (Aiken et al. 1983; 1985), but there is no evidence from field studies to suggest that this has been the case (Campbell and Brattey 1986). In the Bay of Fundy the incidence of infestation appears to have declined significantly in the last 3 yr (S. L. Waddy, unpubl.).

## Larvae and Postlarvae

For obvious reasons, most data on survival, growth, and development of larval (stages I–III) and postlarval lobsters (stages IV, V) have come from laboratory studies. Although

survival, growth, and development rates in captivity may differ from those in the wild, controlled laboratory conditions demonstrate the relative effects of the many factors that can influence larval growth. These include food, light, temperature, salinity, disease, mutilation, social environment, substrate, and water quality (Aiken 1980; Phillips and Sastry 1980; Sastry and Pechenik 1977). The more important of these are discussed in the following sections.

### Temperature

When nutrition and space are adequate, temperature seems to have the most significant effect on the rate of larval development. Time from hatching to stage IV is approximately 10 d at 22–24°C and nearly 2 mo at 10°C. At 5°C, larvae generally die without reaching stage IV (Templeman 1936c).

Unlike embryo development, larval development cannot be completed at low temperature, so it is important that hatching occur before the water temperature declines. This is especially important at the northern limits of the lobster's range.

The literature contains conflicting information on the effect of temperature on larval size. Hadley (1906) stated that higher rearing temperatures produce larger larvae, but it has been said that larvae from offshore areas (generally cooler) are larger than those from inshore areas (Rogers et al. 1968). Templeman (1948) reported that stage IV postlarvae from a cold-water area were larger than those from a warmwater area, but B. MacKenzie (pers. comm.) reared larvae from females taken from the warm waters of Northumberland Strait (southern Gulf of St. Lawrence) and the cold oceanic waters off southwest Nova Scotia and found no consistent relationship between larval origin and size at stage V. However, he did find that larvae reared at 15–18°C were consistently larger than those reared at 10, 12, or 22°C.

In some species the minimum temperature required for larval metamorphosis varies with season (Sastry and Vargo 1977) but no seasonal variation has been identified in *Homarus*. Nor does size at stage IV appear to be affected by season (Aiken et al. 1982). Although the first larvae hatched from a brood are consistently the largest of the siblings when they reach stage IV (Aiken et al. 1981), such developmental differences among sibling larvae may be simply a reflection of the known biochemical and energy differences in larvae hatched on successive days (Sastry and Pechenik 1977).

Caddy (1976) suggested that peak larval survival in Northumberland Strait occurs at approximately 11°C and that the molt to stage IV probably occurs no later than the end of August. He contrasted this with the waters off southwest Nova Scotia, in which he thought larval development would extend well beyond August because the degree-day requirement for completion of larval development increases with declining temperature. This phenomenon would effectively limit the period in which hatching could occur and still result in benthic postlarvae. Caddy further postulated that attainment of stage V would be postponed indefinitely unless the daily increment to the temperature sum exceeds 33 times the daily decline in mean surface temperature.

### Stress

Cobb (1968) initially thought that stage IV postlarvae could delay molting when exposed to substrates unsuitable for settlement, but he subsequently showed this to be the result of social interaction, not substrate type (Cobb 1970). However, stage IV lobsters will delay settlement if faced with unsuitable habitat (Botero and Atema 1982; Cobb et al. 1983). When the bottom is unsuitable the lobster will continue a succession of "touchdowns and liftoffs" until suitable substratum is encountered (J. S. Cobb, pers. comm.).

Unsuitable environment can also affect earlier larval stages. Templeman (1936b) described a larval form intermediate between stage III and IV that retained functional appendages from the earlier stage (Fig. 3). These intermediate forms occurred when environmental conditions were stressful or otherwise unfavorable. The intermediates could molt to a normal stage or to further intermediate stages, effectively delaying metamorphosis. Although these larvae eventually complete metamorphosis (Charmantier et al. 1985a), the delay increases their exposure to predation, declining temperature, and other factors that affect survival.

### Anthropogenic Changes

Human impact on the environment can alter larval recruitment patterns and success. The construction of a causeway on the Strait of Canso is believed by some to have reduced lobster recruitment on the eastern shore of Nova Scotia by altering larval dispersal (Dadswell 1979; Harding et al. 1983; but see Robinson 1979). The causeway may also have had an indirect effect on growth, reproduction, survival, and recruitment by reducing the genetic mixing of lobsters from the Gulf of St. Lawrence and the eastern shore of Nova Scotia.

Tidal power plants, with their capacity to alter currents and flux, could have local effects on larval survival and distribution, or on the movements or distribution of larger lobsters, which could in turn alter larval distribution.

Poor agricultural practices adjacent to areas such as Northumberland Strait can produce siltation and turbidity that can destroy lobster habitat and adversely affect larval growth, development, and survival. Quarrying, dredging, construction in nearshore areas, and drilling for oil can also increase turbidity and alter the marine environment.

Effluent from conventional and nuclear power plants can alter thermal patterns and have local effects on larval survival, growth, and development (Sastry 1980), and some larval stages are more sensitive than others. Stage II larvae, for example, have a much lower upper temperature tolerance limit than other stages (Sastry and Vargo 1977).

Embryos and larvae are also very sensitive to contaminants. Larvae are 14–1000 times more susceptible than adults (Connor 1972), and stage I larvae are usually the most sensitive of the larval stages. The deleterious effects of petroleum products, industrial chemicals, and heavy metals have been described (for reviews see Phillips and Sastry 1980; Fingerman 1985; see also Capuzzo et al. 1984; Charmantier et al. 1985b; Derby and Capuzzo 1984; McLeese 1974b, 1976; McLeese and Metcalfe 1979).

Reduced survival, growth, and regeneration, increased incidence of malformation, delayed development, changes in metabolism and energetics, inhibition of molting, and presence of intermediate stages have all been associated with exposure to such pollutants. In addition, investigators have found a synergism between pollutants and natural environmental stresses (Fingerman 1985).

### Other Factors

#### *Season*

Under laboratory conditions, lobster larvae that hatch late in

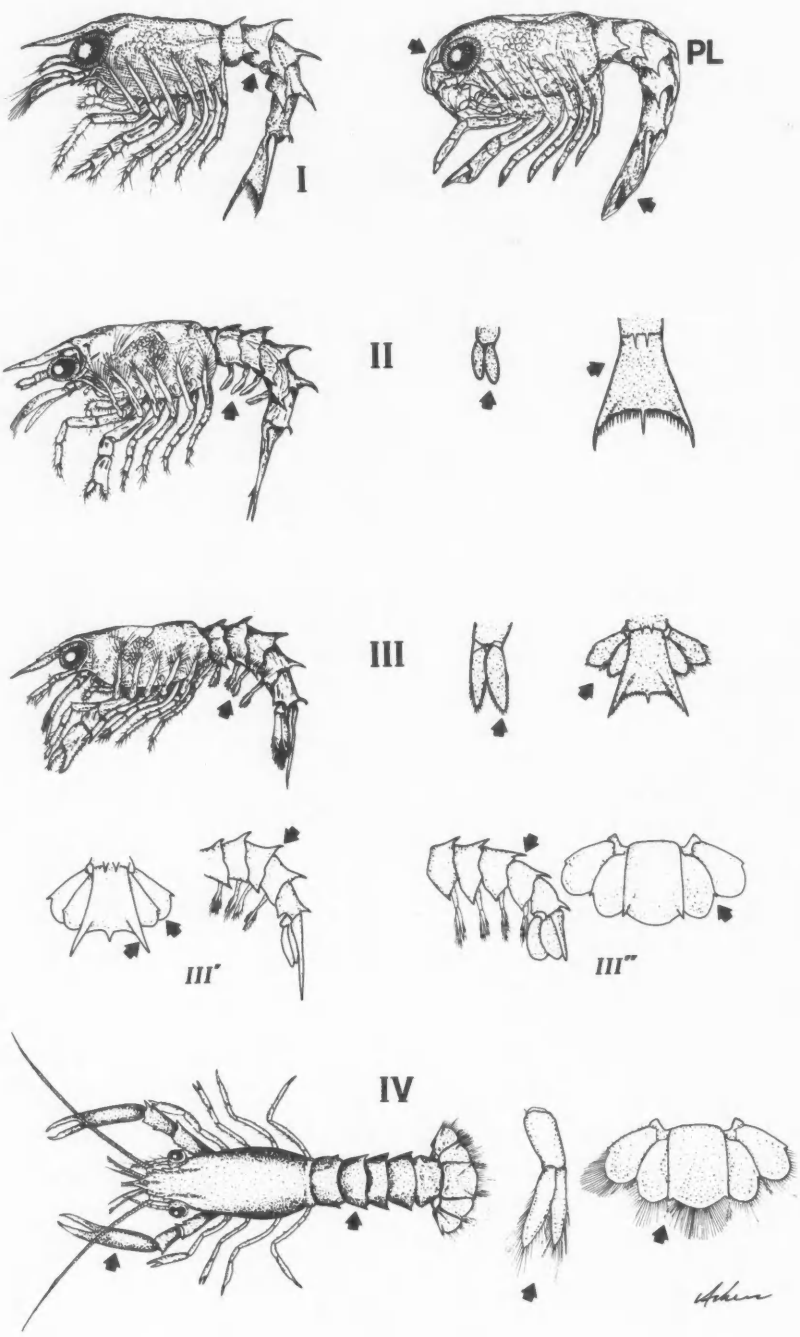


FIG. 3. Normal and intermediate larval stages leading to the first postlarval stage (IV) of the American lobster. Stages PL, I, II, and III are normal larval forms. Characters designated III′ and III″ are intermediate between stages III and IV and occur under adverse environmental conditions. Diagnostic characters for each stage are indicated by arrows.

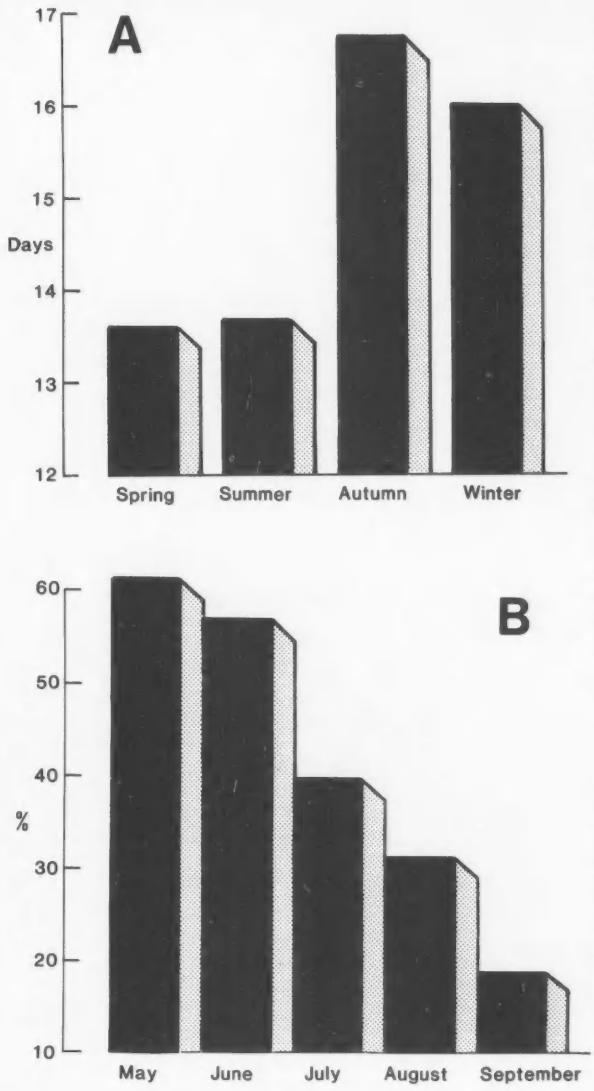


FIG. 4. Effect of season on (A) rate of development and (B) percent survival to stage IV of larval American lobsters reared in a culture facility at constant 20°C.

the season (autumn, winter) take longer to reach stage IV than those that hatch in spring and summer (Fig. 4A), even when temperatures are identical (Aiken et al. 1982). Development time can be modified by both season and photoperiod: in spring the most rapid development occurs in very short days (LD 01:23), but in late summer the most rapid development occurs in very long days (LD 23:01).

Larval survival to stage IV in Northumberland Strait appears to be greatest for larvae hatched early in the season (Caddy 1976), and data from larvae reared in the laboratory support this conclusion (Fig. 4B). In this context it has been suggested that inshore movement of ovigerous females to warmer water in spring enhances larval survival by advancing the time of larval release (Campbell 1986; Campbell and Stasko 1986).

*Salinity*

When the embryo hatches it sheds its relatively impermeable external membrane and becomes a stage I larva, isoionic and sensitive to abrupt changes in salinity. This condition persists until stage IV, at which time the lobster becomes slightly hyperionic and correspondingly more able to survive in reduced salinity (Charmantier et al. 1984b).

Larval lobsters appear to suffer when the salinity drops much below 19–20 ppt (Templeman 1936c), a level easily reached in local surface waters following a heavy rainfall, but Scarratt and Raine (1967) found that larvae would avoid salinities of 21–22 ppt. From this they concluded that low surface salinity would not necessarily be harmful to larvae.

*Food*

Larval lobsters require relatively more food than adults (Thorson 1950), and those that have more food develop faster, grow larger, and survive better (Carlberg and Van Olst 1976; Eagles et al. 1986; Templeman 1936c). Larval mortality can also be caused by poor food quality and other factors that prolong development time and thus increase exposure to predation and disease (Thorson 1950; Scarratt 1964). Experiments using fragmented or carotenoid-deficient frozen adult *Artemia* as food for larval lobsters support the principle that poor food quality increases development time and decreases growth of decapod larvae. Availability of food is particularly important for newly hatched stage I larvae (Eagles et al. 1986), and the animal's ability to withstand starvation may be related to yolk reserves remaining when the larva hatches (Sasaki et al. 1986).

*Wind and currents*

Several hypotheses relate larval drift to residual surface currents, which would enhance distribution and dispersal (Dadswell 1979; Harding et al. 1983). Conversely, Templeman (1939, 1940b) suggested that offshore winds carry larvae away from the east coast of Newfoundland into cold offshore waters where few would be likely to survive. Cobb et al. (1983) found concentrations of larval and postlarval lobsters in areas where currents converge and produce zones of strong vertical motion called downwelling. The fact is, little of substance is known about the effect of wind and surface (or subsurface) currents on larval survival, growth, rate of development, or dispersal. This is a subject that deserves much more attention.

## Juveniles and Adults

### Temperature

Of all the environmental parameters, temperature has the most pervasive influence on survival, growth, and reproduction of juvenile and adult lobsters. The effects can be direct, e.g. synchronization of molting and reproduction, or indirect, as in the effect that temperature has on the epidemiology of certain diseases that affect lobster survival.

*Survival*

Long-term cycles in water temperature appear to influence the number of lobsters that survive to market size, but the mechanism for this is unknown (Ennis 1986 for review). Significant short-term temperature variations are common in the natural environment, but are seldom lethal. Juvenile and adult lobsters exist at water temperatures that vary seasonally from less than 0°C to approximately 25°C. They are extremely tolerant of abrupt temperature changes and within certain ranges

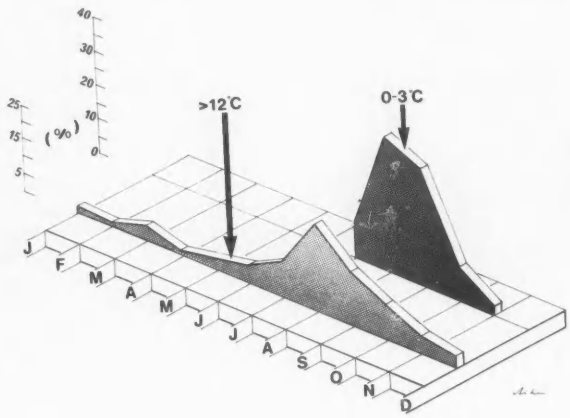


FIG. 5. Effect of winter seawater temperature on synchrony of molting in the American lobster. When winter temperature is no lower than 12°C, molting can occur in all months of the year. When winter temperature is 0–3°C, molting is concentrated in the summer and autumn months.

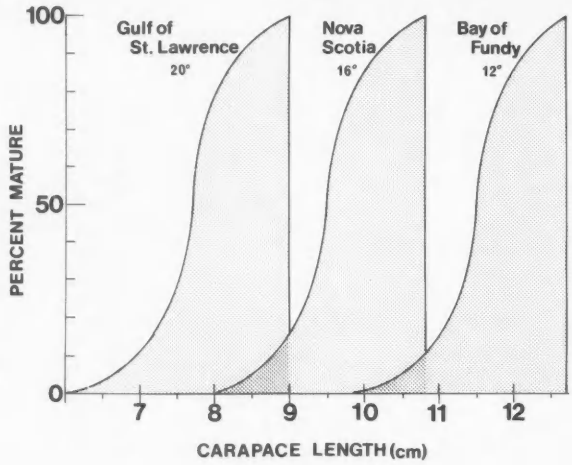


FIG. 6. Size at maturity of female American lobsters from areas with different summer seawater temperatures.

can survive rapid increases of 16°C and decreases of 20°C (McLeese 1951, 1956).

*Molting and growth*

Juvenile growth rate is proportional to temperature, and molting occurs about 1 wk later for each degree of reduction in the mean summer water temperature (Templeman 1936a, 1940b). The proportion of lobsters of a given size that molt each year is higher in warmwater areas and can vary from year to year (Ennis 1983b). In particularly cold years the proportion that molt can decrease by almost 50% (see Campbell 1983).

Offshore lobsters molt over a much greater part of the year than nearshore lobsters, presumably because the annual temperature regimes of offshore waters are relatively uniform (Cooper 1977b) and higher winter water temperature tends to desynchronize molting (Fig. 5). Offshore lobsters are also assumed to grow faster than inshore lobsters and to become recruits to the fishery after 4–5 yr instead of the 7–12 yr required by those that stay in nearshore waters (Cooper 1977b).

Metabolic processes are accelerated by elevated temperature, and temperatures between 8 and 25°C have a direct effect on molt frequency. When water temperature drops to approximately 5°C, induction of active premolt (molt stage $D_1$) is blocked. Lobsters have been prevented from passing from molt stage $D_0$ into $D_1$ for nearly 3 yr by maintaining the temperature at 5°C or less (Aiken 1980). However, those that reach stage $D_1$ before the temperature drops to 5–6°C will continue slowly through premolt and can successfully complete ecdysis at temperatures as low as 0°C (Aiken and Waddy 1976). Those in earlier molt stages continue to develop slowly until they reach $D_0$, where they remain until the temperature again increases. To a large extent, this phenomenon is responsible for the synchrony of the spring molt of inshore lobsters.

Length increment at molt is relatively consistent from year to year for lobsters in a given locality (Conan 1978; Ennis 1971, 1972; compare Campbell 1983), but it can vary significantly between areas (for references see Ennis 1972, 1986; compare Wilder 1953; Conan 1978) and tends to be slightly greater in the warm waters of the southern Gulf of St. Lawrence than in the colder Bay of Fundy (Wilder 1953).

However, onset of maturity also is accelerated by higher temperatures, and maturity has a negative effect on both molt frequency and linear increase. This can distort the impression of growth rate over the long term. For example, lobsters from warmwater areas grow faster than lobsters from colder areas, but since the warmwater lobsters mature at a smaller size, the impression given by von Bertalanffy growth equations is that cold-water lobsters grow faster (Ennis 1986 for review).

*Matuation and spawning*

There is considerable geographic variation in size at onset of sexual maturity in lobsters (Fig. 6; see Aiken and Waddy 1980 for review). As Templeman (1936a) noted, high summer temperature favors early maturation, and low summer temperature delays onset of maturity. Laboratory studies have since verified that higher temperatures are associated with earlier maturation in both males and females. However, the winter period of low temperature seems to be important, as continuous high temperature is detrimental to the production of gametes (Aiken et al. 1984; Waddy and Aiken 1984b).

The first spawning year is the Adult-I year. A mature female will normally spawn one summer and molt the next, but approximately 20% of the maturing Adult-I females from warmwater areas molt and then spawn shortly after (Aiken and Waddy 1982). This is rare in the Adult-II or subsequent years and uncommon among Adult-I lobsters from cold-water areas. Thus, the Adult-I molt–spawn phenomenon is more common in the southern Gulf of St. Lawrence than along the Atlantic coast of Nova Scotia (Robinson 1979; Templeman 1940a). A similar situation exists in Newfoundland waters (Ennis 1980, 1984b).

Offshore lobsters winter in the canyons of the continental slope, but in summer they move to shallow (and warmer) portions of the shelf and coastal areas where their reproductive cycle is completed (Campbell et al. 1984; Cooper 1977a; Cooper and Uzmann 1980; Fogarty et al. 1980; Uzmann et al.

1977). It has been postulated that the offshore temperatures are too low for spawning and molting to be properly synchronized and that seasonal movements allow the animals to remain within an optimum temperature range of 8–14°C (Cooper and Uzmann 1980).

Large female lobsters show a greater tendency toward purposeful movements from one area to another than smaller, immature lobsters (Dow 1974; Morrissey 1971; Stasko 1978). According to Saila and Flowers (1968), ovigerous lobsters that were moved from continental shelf waters tended to return to their area of capture after their eggs hatched. Recent tag–recapture results (Pezzack and Duggan 1986) suggest similar seasonal movements in the Browns Bank area of the Scotian Shelf.

Lobsters in the nearshore zone, although considered by some to be nonmigratory (Cooper and Uzmann 1980 for review), typically move to deeper water as the temperature declines in winter and return to shallow water as the temperature increases in spring (Campbell 1984, 1986; Ennis 1983a, 1984a; Herrick 1909; Munro and Therriault 1983). Mature females tend to move sooner, further, and deeper. Campbell and Stasko (1986) postulated that seasonal shallow–deep movements in some areas optimize the degree-day situation for molting, growth, gonadal development, and embryo development.

## Stress

In some areas the percentage of sublegal sized lobsters in the catch may reach 80% toward the end of the fishing season (Elner 1980 for references). An intense fishery and large catches of sublegal and ovigerous lobsters can increase the likelihood of predation and poaching and result in increased egg loss, injury, handling stress, decreased molt frequency, and reduced linear increment (Emmel 1906; Ennis 1971; Wilder 1965; Brown and Caputi 1986a, 1986b; Hunt and Lyons 1986; Lyons 1986; S. L. Waddy, unpubl.). Heavy fishing pressure also means a greater incidence of lost traps, and "ghost fishing" by such traps can result in substantial numbers of entrapped lobsters (Smolowitz and Serchuk 1980).

Lobsters are also displaced, injured, or killed by scallop dredges, Irish moss rakes, and a variety of large trawl gear. Scarratt (1973) estimated that up to 280 lobsters can be killed or maimed per boat-day of such activity.

In recent years there has been increased fishing effort both offshore (Pezzack and Duggan 1983) and in marginally productive inshore areas (Ennis 1982a), and "jumbo" lobsters 120 mm carapace length (CL) and larger are now being trapped near Grand Manan (Campbell and Duggan 1980), along the Atlantic coast of Nova Scotia, and in Northumberland Strait (Elner 1980). Fishing has thus become both intensive and extensive, and this will affect survival, growth, and recruitment in ways that may not be apparent for years.

## Disease, Parasitism, and Predation

### *Fungal and bacterial infections*

The bacterium *Aerococcus viridans* causes the fatal infection gaffkemia. It is common in wild stocks, and a high incidence of natural infection has been recorded. Stewart (1978) suggested that gaffkemia epidemics can infect up to 40% of a local population. Under laboratory conditions, infections are invariably fatal, and lobsters of all ages are equally susceptible (Stewart 1980). However, the impact of this pathogen on lobster stocks is not known.

Shell disease, which erodes the exoskeleton and can cause death in severe cases, can affect wild lobsters, but it is maily a disease of lobsters impounded in areas with poor water quality. However, in heavily polluted areas there can be a high incidence of shell disease (Young and Pearce 1975). Shell "disease" is a syndrome caused by chitinoclastic microorganisms, but there is divided opinion as to the taxa involved. In Europe the causative agents are considered to be several different fungi, but in North America, bacteria are implicated (see Stewart 1980, 1984 for reviews). Malloy (1978) produced the necrotic lesions of shell disease with a *Vibrio* (*Beneckea*) bacterium that had been isolated from lobsters with shell disease.

At least two fungi can infect and kill cultured juvenile lobsters. *Fusarium* can penetrate gill lamellae and cause respiratory distress, and *Haliphthoros* has been found in the branchial chamber and surrounding tissues and in the articular membranes of the joints. Neither of these organisms has been identified with lobster pathology in the natural environment (Stewart 1984).

### *Parasitism*

Many parasites are associated with lobsters, but most are relatively harmless (Stewart 1980, 1984 for reviews). Montreuil (1954) and Brattey and Campbell (1986) suggested that larval acanthocephalans might be responsible for a chronic low-level lethal effect on lobsters, but there has been no confirmation of this. Although the branchiobdellid annelid *Histriobdella homari* is usually considered benign, and no pathological effects were identified even in lobsters carrying over 600 *H. homari*, Brattey and Campbell (1985) postulated that heavy infestation (>200 per lobster) might reduce respiratory flow across the gills. They also cited Sindermann (1977) as suggesting that this organism might reduce the hatching success of lobster embryos.

A blood ciliate similar to the *Anophrys* found in crabs infects wild as well as impounded lobsters (Aiken et al. 1973). Natural incidence and prevalence are unknown, but it appears to be cyclic. We have found it in wild stocks three times in the past 14 yr (Fig. 7). All cases occurred during winter when the water temperature was 0–5°C. Infection can be transferred by injection of hemolymph from infected animals, and death will occur within 6–8 wk if the water temperature remains low. A similar protozoan found in crabs is thought to be free-living under normal conditions (Sindermann 1977).

### *Predation*

Larval and postlarval lobsters are subject to heavy predation, but once the postlarval animal becomes benthic and burrows into the substratum it is relatively free from predation until approximately 20–45 mm CL, at which size it begins to leave the burrow for active foraging (Cooper and Uzmann 1977; P. Lawton, pers. comm.). At this size it is suitable prey for sculpin, cunner, tautog, black sea bass, and sea raven (Cooper and Uzmann 1977). Lobsters larger than 50 mm CL can be difficult prey, but Atlantic cod, wolffish, goosefish, tilefish, and several species of sharks consume lobsters up to 100 mm CL (Cooper and Uzmann 1977; Herrick 1909). Predation is greater where shelter is limited. Unlike crabs, which can escape predators by burrowing rapidly, lobsters require access to existing refuge (Richards and Cobb 1986).

Under natural conditions, predation by other lobsters is rare, even during the molting season (Atema and Cobb 1980; Cooper and Uzmann 1977). The combination of legal fishing activity

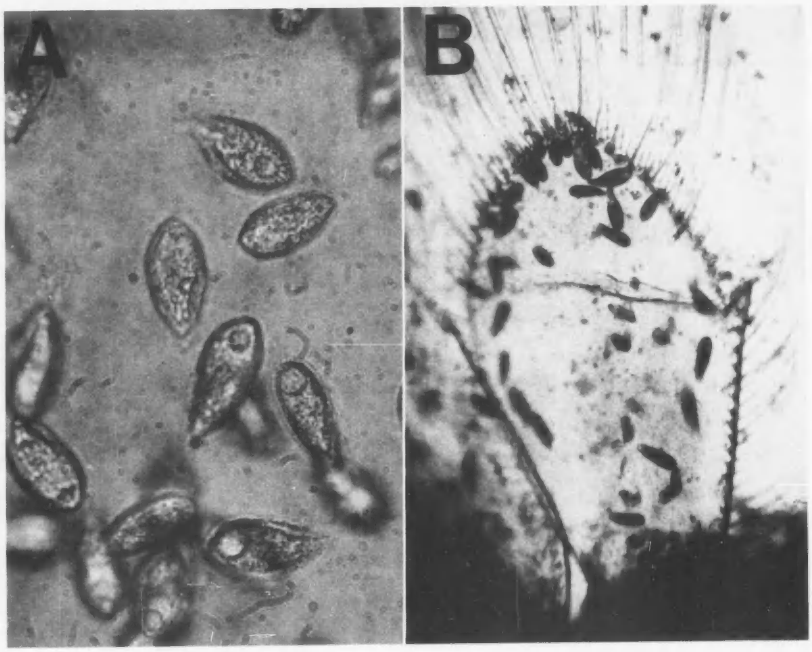


FIG. 7. Infestation of the hemolymph of the American lobster by an unidentified ciliate protozoan. (A) Consuming hemocytes of adult lobster; (B) inside the uropod of a stage V lobster, from which the hemocytes and much of the soft tissue have been consumed.

plus poaching and bycatches in trawl and seine fisheries has made man the major predator on juvenile and adult lobsters (Campbell 1980; Wilder 1965).

## Anthropogenic Changes

The acute effects of lethal chemicals in the marine environment are easily recognized, but sublethal effects are deleterious and much less apparent. When exposure persists, physiological processes can be altered (Sastry and Miller 1981 for review). Unfortunately, the few existing physiological studies on lobsters were done on larval stages, so little is known about the physiological effects of contaminants on juveniles and adults.

Lobsters adjacent to the heavily industrialized areas of the northeastern United States are exposed to many pollutants. The acute and sublethal effects of industrial discharges such as bleached kraft mill effluent, yellow phosphorus, potash brine, drilling muds, and other pollutants including creosote, heavy metals, pesticides, and crude and refined oils have been studied. Some of the identified sublethal effects include reduced survival, growth, and regeneration, changes in ATPase activity, increased oxygen consumption in gill tissue, increased susceptibility to disease, thinning of shells, morphological abnormalities, inability to molt, and changes in behavior (Aiken and Byard 1972; Atema 1977; Atema and Stein 1972; Barshaw and Atema 1984; Charmantier et al. 1985b; Fingerman 1985; Haya et al. 1983; McLeese 1974a, 1974b, 1976; McLeese et al. 1980; McLeese and Metcalfe 1979; Sprague and McLeese 1968; Thurberg et al. 1977).

In addition to their direct effects, pollutants can change the habitat. Ocean dumping can cause changes in bathymetry, sediment grain size, and trace element concentration, causing chronic disturbances to benthic biota and the structure of populations (Elner and Hamet 1984; Oostdam 1983), and when heavy oils are incorporated into the sediments, oil-soaked gravel "pavement" may develop (Scarratt 1974).

## Other Factors

### *Salinity*

Juvenile and adult lobsters have been found to survive well in salinities above approximately 10 ppt (McLeese 1956; Charmantier et al. 1984a). Since freshwater tends to lie above saline water, and lobsters are normally found on the bottom, this degree of tolerance would seem adequate protection from low saline conditions except during ecdysis. However, Thomas and White (1969) reported one instance of overwintering lobsters in the Gulf of St. Lawrence being killed in their burrows when heavy spring runoff combined with strong winds to drive the freshwater layer 3 m deep.

### *Habitat*

Laboratory and field studies have demonstrated that the size range of lobsters found in a habitat is determined by the niche size provided by the substrate (Aiken 1980; Cobb 1971; Howard 1980; Scarratt 1968). The importance of substrate and shelter has been further demonstrated by the increase in numbers of lobsters that follows construction of an artificial reef (Briggs and Zawacki 1974; Scarratt 1968; Sheehy 1976).

Mann and co-workers (Miller 1985 for references) have suggested that a dense growth of macrophytes adds needed complexity to a rock habitat and shelters juvenile lobsters from

predators. The loss of seaweed beds has been blamed for a decline in lobsters along the south coast of Nova Scotia, but this hypothesis has been challenged (Miller 1985).

Juvenile lobsters are known to have distinct substrate preferences, but appear able to adapt to a variety of habitats. Juveniles can inhabit an existing crevice, excavate a burrow under a rock, or (in the case of *H. gammarus*) develop an extensive burrow system in cohesive mud (Howard and Bennett 1979). Such flexibility increases the opportunities for settlement and growth during the vulnerable early stages of juvenile life.

## Summary

The recruitment cycle starts with the germinal epithelium and progresses through successive life stages until the lobster enters the fishery. To complete the recruitment cycle the lobster population must survive, grow, and reproduce, so anything that affects these biological processes also affects recruitment.

Of the environmental factors known to affect recruitment, temperature and disease are the most significant. Anthropogenic changes to the environment are somewhat less important, and a number of others, including nutritional, hydrological, and meteorological conditions, are considered secondary because their influence is usually limited to small areas or brief periods of time.

However, all unfavorable environmental conditions cause stress, and stress exaggerates the impact of an adverse environment. Contaminants in sublethal concentrations can stress the lobster and make it more susceptible to disease or less able to withstand meteorological or hydrological situations that would not normally be a problem. The stress of capture, handling, and return to the water during trapping in the lobster fishery and from exposure to trawl, dredging, and raking gear used in other fisheries has debilitating effects other than physical injury that are difficult to quantify.

Recruitment is a function of heredity and environment. Heredity gives an individual (and a population) a range of tolerance for environmental situations, and the environment applies the selective pressures against those limits. When the limits are exceeded, a life stage, an individual, or — in extreme cases — a population will be lost.

## References

AIKEN, D. E. 1980. Molting and growth, p. 91–162. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

AIKEN, D. E., AND E. H. BYARD. 1972. Histological changes in lobsters (*Homarus americanus*) exposed to yellow phosphorous. Science (Wash., DC) 176: 1434–1435.

AIKEN, D. E., D. J. MARTIN, J. D. MEISNER, AND J. B. SOCHASKY. 1981. Influence of photoperiod on survival and growth of larval American lobsters (*Homarus americanus*). J. World Maricult. Soc. 12: 225–230.

AIKEN, D. E., W. J. ROWE, D. J. MARTIN-ROBICHAUD, AND S. L. WADDY. 1982. Seasonal differences in the effect of photoperiod on survival and development of larval American lobsters (*Homartus americanus*). J. World Maricult. Soc. 13: 287–293.

AIKEN, D. E., J. B. SOCHASKY, AND P. G. WELLS. 1973. Ciliate infestation of the blood of the lobster *Homarus americanus*. Int. Counc. Explor. Sea C.M. 1973/K:46.

AIKEN, D. E., AND S. L. WADDY. 1976. Controlling growth and reproduction in the American lobster. Proc. World Maricult. Soc. 7: 415–430.

1980. Reproductive biology, p. 215–276. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

1982. Cement gland development, ovary maturation, and reproductive cycles in the American lobster *Homarus americanus*. J. Crustacean Biol. 2: 315–327.

1985a. The uncertain influence of spring photoperiod on spawning in the American lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 42: 194–197.

1985b. Photoperiodic control of vitellogenesis in the American lobster (*Homarus americanus*): comment on a recent report. Can. J. Fish. Aquat. Sci. 42: 198–199.

1985c. Production of seed stock for lobster culture. Aquaculture 44: 103–114.

1986. Oocyte maturation and spawning in wild American lobsters (*Homarus americanus*): lack of evidence for significant regulation by photoperiod. Can. J. Fish. Aquat. Sci. 43: 1451–1453.

AIKEN, D. E., S. L. WADDY, K. MORELAND, AND S. M. POLAR. 1984. Electrically induced ejaculation and artificial insemination of the American lobster *Homarus americanus*. J. Crustacean Biol. 4: 519–527.

AIKEN, D. E., S. L. WADDY, AND L. S. UHAZY. 1985. Aspects of the biology of *Pseudocarcinonemertes homari* and its association with the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 351–356.

AIKEN, D. E., S. L. WADDY, L. S. UHAZY, AND A. CAMPBELL. 1983. A nemertean destructive to the eggs of the lobster, *Homarus americanus*. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 182: 130–133.

ATEMA, J. 1977. The effects of oil on lobsters. Oceanus 20: 67–73.

ATEMA, J., AND J. S. COBB. 1980. Social behavior, p. 409–450. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

ATEMA, J., AND L. STEIN. 1972. Sublethal effects of crude oil on lobster (*Homarus americanus*) behavior. Technical report prepared for EPA contract EBN 18080. NITS, Dep. Commer. No. PB-213 872: 40 p.

BARSHAW, D. E., AND J. ATEMA. 1984. Effects of drilling mud on the behavior, growth, and survival of young juvenile lobster (*Homarus americanus*). Biol. Bull. 167: 506 p.

BOTERO, L., AND J. ATEMA. 1982. Behavior and substrate selection during larval settling in lobster *Homarus americanus*. J. Crustacean Biol. 2: 59–69.

BRATTEY, J., AND A. CAMPBELL. 1985. Occurrence of *Histriobdella homari* (Annelida: Polychaeta) on the American lobster in the Canadian maritimes. Can. J. Zool. 63: 392–395.

1986. A survey of parasites of the American lobster, *Homarus americanus* (Crustacea: Decapoda), from the Canadian Maritimes. Can. J. Zool. 64. (In press)

BRATTEY, J., A. CAMPBELL, A. E. BAGNALL, AND L. S. UHAZY. 1985. Geographic distribution and seasonal occurrence of the nemertean *Pseudocarcinonemertes homari* on the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 360–367.

BRIGGS, P. T., AND C. S. ZAWACKI. 1974. American lobsters at artificial reefs in New York. N.Y. Fish Game J. 21: 73–77.

BROWN, R. S., AND N. CAPUTI. 1986a. Conservation of recruitment of the western rock lobster (*Panilirus cygnus*) by improving survival and growth of undersize rock lobsters captured and returned by fishermen to the sea. Can. J. Fish. Aquat. Sci. 43: 2236–2242.

1986b. Factors affecting the growth of undersize western rock lobster, *Panulirus argus* George, returned by fisherman to the sea. U.S. Dep. Commer. Fish. Bull. 83: 567–574.

CADDY, J. F. 1976. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence. ICES Special Meeting Population Assessment of Shellfish Stock, Paper No. 10: 44 p. (Available from Library, Biological Station, St. Andrews, N.B. E0G 2X0)

CAMPBELL, A. 1980. A review of mortality estimates of lobster populations in the Canadian Maritimes. Can. Tech. Rep. Fish. Aquat. Sci. 932: 27–36.

1983. Growth of tagged lobsters (*Homarus americanus*) off Port Maitland, Nova Scotia, 1945–80. Can. Tech. Rep. Fish. Aquat. Sci. 1232: 10 p.

1984. Aspects of lobster biology and fishery in the upper reaches of the Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1256: 469–488.

1986. Migratory movements of ovigerous lobsters, *Homarus americanus*, tagged off Grand Manan, eastern Canada. Can. J. Fish. Aquat. Sci. 43: 2197–2205.

CAMPBELL, A., AND J. BRATTEY. 1986. Egg loss from the American lobster, *Homarus americanus*, in relation to nemertean, *Pseudocarcinonemertes homari*, infestation. Can. J. Fish. Aquat. Sci. 43: 772–780.

CAMPBELL, A., AND D. R. DUGGAN. 1980. Review of the Grand Manan lobster fishery with an analysis of recent catch and effort trends. Can. Tech. Rep. Fish. Aquat. Sci. 997: 20 p.

CAMPBELL, A., D. E. GRAHAM, H. J. MACNICHOL, AND A. M. WILLIAMSON. 1984. Movements of tagged lobsters released on the continental shelf from

Georges Bank to Baccaro Bank, 1971–1973. Can. Tech. Rep. Fish. Aquat. Sci. 1288: 16 p.

CAMPBELL, A., AND D. G. ROBINSON. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian maritimes. Can. J. Fish. Aquat. Sci. 40: 1958–1967.

CAMPBELL, A., AND A. B. STASKO, 1986. Movements of lobsters (*Homarus americanus*) tagged in the Bay of Fundy, Canada. Mar. Biol. (In press)

CAPUZZO, J. M., B. A. LANCASTER, AND G. A. SASAKI. 1984. The effects of petroleum hydrocarbons on lipid metabolism and energetics of larval development and metamorphosis in the American lobster (*Homarus americanus* Milne-Edwards). Mar. Environ. Res. 14: 201–228.

CARLBERG, J. M., AND J. C. VAN OLST. 1976. Brine shrimp (*Artemia salina*) consumption by the larval stages of the American lobster (*Homarus americanus*) in relation to food density and water temperature. Proc. World Maricult. Soc. 7: 379–389.

CASTELL, J. D., AND S. D. BUDSON. 1974. Lobster nutrition: the effect on *Homarus americanus* of dietary protein levels. J. Fish. Res. Board Can. 31: 1363–1370.

CASTELL, J. D., AND J. C. KEAN. 1986. Evaluation of the role of nutrition in lobster recruitment. Can. J. Fish. Aquat. Sci. 43: 2320–2327.

CHARMANTIER, G., M. CHARMANTIER-DAURES, AND D. AIKEN. 1984a. Neuroendocrine control of hydromineral regulation in the American lobster *Homarus americanus* H. Milne-Edwards 1837 (Crustacea, Decapoda). 1. Juveniles. Gen. Comp. Endocrinol. 54: 8–19.

1984b. Neuroendocrine control of hydromineral regulation in the American lobster *Homarus americanus* H. Milne-Edwards 1837 (Crustacea, Decapoda) 2. Larval and postlarval stages. Gen. Comp. Endocrinol. 54: 20–34.

1985a. Intervention des pédoncules oculaires dans le contrôle de la métamorphose chez *Homarus americanus* H. Milne-Edwards, 1837 (Crustacea, Decapoda). C.R. Acad. Sci. Paris 300 (Ser. III): 271–276.

CHARMANTIER, G., M. CHARMANTIER-DAURES, AND W. W. YOUNG-LAI. 1985b. Lethal and sublethal effects of potash brine on different stages of the lobster, *Homarus americanus*. Can. Tech. Rep. Fish. Aquat. Sci. 1344: 13 p.

COBB, J. S. 1968. Delay of moult by the larvae of *Homarus americanus*. J. Fish. Res. Board Can. 25: 2251–2253.

1970. Effect of solitude on time between fourth and fifth larval molts in the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 27: 1653–1655.

1971. The shelter-related behavior of the lobster, *Homarus americanus*. Ecology 52: 108–115.

COBB, J. S., T. GULBRANSEN, B. F. PHILLIPS, D. WANG, AND M. SYSLO. 1983. Behavior and distribution of larval and early juvenile *Homarus americanus*. Can. J. Fish. Aquat. Sci. 40: 2184–2188.

CONAN, G. Y. 1978. Comparison between growth at molt of the European and American lobsters in different geographical locations, according to sex and state of maturity. Int. Counc. Explor. Sea C.M. 1978/K:18.

CONNOR, P. M. 1972. Acute toxicity of heavy metals to some marine larvae. Mar. Pollut. Bull. 3: 190–192.

COOPER, R. A. 1977a. Ecology of shallow and deep water American lobsters (*Homarus americanus*) from the New England continental shelf. CSIRO Div. Fish. Oceanogr. (Aust.) Circ. 7: 27–28.

1977b. Growth of deep water American lobsters (*Homarus americanus*) from the New England continental shelf. CSIRO Div. Fish. Oceanogr. (Aust.) Circ. 7: 35.

COOPER, R., AND J. R. UZMANN. 1977. Ecology of juvenile and adult clawed lobsters, *Homarus americanus*, *Homarus gammarus*, and *Nephrops norvegicus*. CSIRO Div. Fish. Oceanogr. (Aust.) Circ. 7: 187–208.

1980. Ecology of juvenile and adult *Homarus*, p. 97–142. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

DADSWELL, M. J. 1979. A review of the decline in lobster (*Homarus americanus*) landings in Chedabucto Bay between 1956 and 1977 with a hypothesis for a possible effect by the canso causeway on the recruitment mechanism of eastern Nova Scotia stocks. Can. Fish. Mar. Serv. Tech. Rep. 834: 113–144.

DERBY, J. G. S., AND J. M. CAPUZZO. 1984. Lethal and sublethal toxicity of drilling fluids to larvae of the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 41: 1334–1340.

DOW, R. L. 1974. American lobsters tagged by Maine commercial fishermen, 1957–1959. U.S. Dep. Commer. Fish. Bull. 72: 622–623.

EAGLES, M. D., D. E. AIKEN, AND S. L. WADDY. 1986. Influence of light and food on larval American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2303–2310.

ELNER, R. W. 1980. Lobster gear selectivity — a Canadian overview. Can. Tech. Rep. Fish. Aquat. Sci. 932: 77–84.

ELNER, R. W., AND S. L. HAMET. 1984. The effects of ocean dumping of dredge spoils onto juvenile lobster habitat: a field evaluation. Can. Tech. Rep. Fish. Aquat. Sci. 1247: 12 p.

EMMEL, V. E. 1906. The relation of regeneration to the molting process of the lobster. R.I. Comm. Inland Fish. Annu. Rep. 36: 258–313.

ENNIS, G. P. 1971. Lobster (*Homarus americanus*) fishery and biology in Bonavista Bay, Newfoundland 1966–70. Fish. Res. Board Can. Tech. Rep. 289: 46 p.

1972. Growth per moult of tagged lobsters (*Homarus americanus*) in Bonavista Bay, Newfoundland. J. Fish. Res. Board Can. 29: 143–148.

1975. Observations on hatching and larval release in the lobster *Homarus americanus*. J. Fish. Res. Board Can. 32: 2210–2213.

1980. Size-maturity relationships and related observations in Newfoundland populations of the lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 37: 945–956.

1981. Fecundity of the American lobster, *Homarus americanus*, in Newfoundland waters. U.S. Dep. Commer. Fish. Bull. 79: 796–800.

1982a. The Newfoundland lobster fishery: a review of statistics, stock status and current management considerations. Can. MS Rep. Fish. Aquat. Sci. 1666: 11 p.

1982b. Fisheries and population biology of lobsters (*Homarus americanus*) at Comfort Cove, Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. 1116: 45 p.

1983a. Observations on the behavior and activity of lobster, *Homarus americanus*, in nature. Can. Tech. Rep. Fish. Aquat. Sci. 1165: 26 p.

1983b. Variation in annual growth in two Newfoundland lobster (*Homarus americanus*) populations in relation to temperature conditions. Int. Counc. Explor. Sea C.M. 1983/K:24.

1984a. Small-scale seasonal movements of the American lobster *Homarus americanus*. Trans. Am. Fish. Soc. 113: 336–338.

1984b. Incidence of molting and spawning in the same season in female lobsters, *Homarus americanus*. U.S. Dep. Commer. Fish. Bull. 82: 529–530.

1986. Stock definition, recruitment variability, and larval recruitment processes in the American lobster, *Homarus americanus*: a review. Can. J. Fish. Aquat. Sci. 43: 2072–2084.

ENNIS, G. P., AND P. W. COLLINS. 1983. A computer program to assess egg production per recruit in a lobster (*Homarus americanus*) populatiuon. Can. Tech. Rep. Fish. Aquat. Sci. 1198: 15 p.

FINGERMAN, S. 1985. Non-metal environmental pollutants and growth, p. 219–234. *In* A. M. Wenner [ed.] Crustacean issues 3. Factors in adult growth. A. A. Balkema, Rotterdam, The Netherlands.

FISHER, W. S., E. H. NELSON, J. F. STEENBERGEN, AND D. V. LIGHTNER. 1978. Microbial diseases of cultured lobsters: a review. Aquaculture 14: 115–140.

FLEMING, L. C., AND R. GIBSON. 1981. A new genus and species of monostiliferous hoplonemerteans, ectohabitant on lobsters. J. Exp. Mar. Biol. Ecol. 52: 79–93.

FOGARTY, M. J., D. V. D. BORDEN, AND H. J. RUSSELL. 1980. Movements of tagged American lobster, *Homarus americanus*, off Rhode Island. U.S. Dep. Commer. Fish. Bull. 78: 771–780.

FOGARTY, M. J., AND R. LAWTON. 1983. An overview of larval American lobster, *Homarus americanus*, sampling programs in New England during 1974–79. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-775: 9–14.

HADLEY, P. B. 1906. Regarding the rate of growth of the American lobster, *Homarus americanus*. R.I. Comm. Inland Fish. Annu. Rep. 36: 153–236.

HARDING, G. C., K. F. DRINKWATER, AND W. P. VASS. 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis. Can. J. Fish. Aquat. Sci. 40: 168–184.

HARDING, G. C., W. P. VASS, AND K. F. DRINKWATER. 1982. Aspects of larval American lobster (*Homarus americanus*) ecology in St. Georges Bay, Nova Scotia. Can. J. Fish. Aquat. Sci. 39: 1117–1129.

HAYA, K., B. A. WAIWOOD, AND D. W. JOHNSTON. 1983. Adenylate energy charge and ATPase activity of lobster (*Homarus americanus*) during sublethal exposure to zinc. Aquat. Toxicol. 3: 115–126.

HERRICK, F. H. 1909. Natural history of the American lobster. Bull. U.S. Bur. Commer. Fish. 29: 149–408.

HOWARD, A. E. 1980. Substrate controls on the size composition of lobster (*Homarus gammarus*) populations. J. Cons. Int. Explor. Mer 39: 130–133.

HOWARD, A. E., AND D. B. BENNETT. 1979. The substrate preference and burrowing behavior of juvenile lobsters (*Homarus gammarus* (L.)). J. Nat. Hist. 13: 433–438.

HUGHES, J. T., AND G. C. MATTHIESSEN. 1962. Observations on the biology of the American lobster *Homarus americanus*. Limnol. Oceanogr. 7: 414–421.

HUNT, J. H., AND W. G. LYONS. 1986. Factors affecting growth and maturation of spiny lobsters, *Panulirus argus*, in the Florida keys. Can. J. Fish. Aquat. Sci. 43: 2243–2247.

JOHNSON, P. W., J. M. SIEBURTH, A. SASTRY, C. R. ARNOLD, AND M. S. DOTY. 1971. *Leucothrix mucor* infestation of benthic crustacea, fish eggs and tropical algae. Limnol. Oceanogr. 16: 962–969.

LYONS, W. G. 1986. Problems and perspectives regarding recruitment of spiny lobsters, *Panulirus argus*, to the south Florida fishery. Can. J. Fish. Aquat. Sci. 43: 2099–2106.

MALLOY, S. C. 1978. Bacteria induced shell disease of lobsters (*Homarus americanus*). J. Wildl. Dis. 14: 2–10.

MCLEESE, D. W. 1951. Factors limiting the survival of the lobster *Homarus americanus* (Milne Edwards). M.Sc. thesis, University Western Ontario, London, Ont.

1956. Effects of temperature, salinity and oxygen on the survival of the American lobster. J. Fish. Res. Board Can. 13: 247–272.

1974a. Olfactory responses and fenithrothion toxicity in American lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 31: 1127–1131.

1974b. Toxicity of copper at two temperatures and three salinities to the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 31: 1949–1952.

1976. Toxicity studies with lobster larvae and adults and a freshwater crayfish. Fish. Res. Board Can. MS Rep. 1384: 15 p.

MCLEESE, D. W., AND C. D. METCALFE. 1979. Toxicity of creosote to larval and adult lobsters and *Crangon* and its accumulation in lobster hepatopancreas. Bull. Environ. Contam. Toxicol. 22: 796–799.

MCLEESE, D. W., C. D. METCALFE, AND V. ZITKO. 1980. Lethality of permethrin, cypermethrin and fenvalerate to salmon, lobster and shrimp. Bull. Environ. Contam. Toxicol. 25: 950–955.

MCLEESE, D. W., AND D. G. WILDER. 1964. Lobster storage and shipment. Bull. Fish. Res. Board Can. 149: 69 p.

MILLER, R. J. 1985. Seaweeds, sea urchins, and lobsters: a reappraisal. Can. J. Fish. Aquat. Sci. 42: 2061–2072.

MONTREUIL, P. 1954. Parasitological investigations. Dep. Pêch. Qué. Rapp. Annu. Stat. Biol. Mar., 1953, Contrib. 50 (Append. V): 69–73.

MORRISSEY, T. D. 1971. Movements of tagged American lobsters, *Homarus americanus*, liberated off Cape Cod, Massachusetts. Trans. Am. Fish. Soc. 100: 117–120.

MUNRO, J., AND J.-C. THERRIAULT. 1983. Migrations saisonnières du homard (*Homarus americanus*) entre la côte et les lagunes des Îles-de-la-Madeleine. Can. J. Fish. Aquat. Sci. 40: 905–918.

NELSON, K. 1986. Photoperiod and reproduction in lobsters (*Homarus*). Am. Zool. 26: 447–457.

NELSON, K., AND D. HEDGECOCK. 1985. Reply to Aiken and Waddy. Can. J. Fish. Aquat. Sci. 42: 199–200.

NELSON, K., D. HEDGECOCK, AND W. BORGESON. 1983. Photoperiodic and ecdysial control of vitellogenesis in lobsters (*Homarus*) (Decapoda, Nephropidae). Can. J. Fish. Aquat. Sci. 40: 940–947.

OOSTDAM, B. L. 1983. Sewage sludge dumping in the mid-Atlantic bight in the 1970s: short-, intermediate-, and long-term effects, p. 313–352. *In* I. W. Duedall, B. H. Ketchum, P. K. Park, and D. R. Kester [ed.] Wastes in the ocean. Vol. 1. Industrial sewage wastes in the ocean. John Wiley & Sons, New York, NY.

PERKINS, H. C. 1971. Egg loss during incubation from offshore northern lobsters (Decapoda: Homaridae). U.S. Dep. Commer. Fish. Bull. 69: 451–453.

1972. Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne-Edwards). U.S. Dep. Commer. Fish. Bull. 70: 95–99.

PEZZACK, D. S., AND D. R. DUGGAN. 1983. The Canadian offshore lobster (*Homarus americanus*) fishery — 1971–1982. Int. Counc. Explor. Sea C.M. 1983/K:34.

1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. 43: 2206–2211.

PHILLIPS, B. F., AND A. N. SASTRY. 1980. Larval ecology, p. 11–57. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

RICHARDS, R. A., AND J. S. COBB. 1986. Competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*): effects of relative size. Can. J. Fish. Aquat. Sci. 43: 2250–2255.

ROBINSON, D. G. 1979. Consideration of the lobster (*Homarus americanus*) recruitment overfishing hypothesis: with special reference to the Canso Causeway. Can. Fish. Mar. Serv. Tech. Rep. 834: 77–99.

ROGERS, B. A., J. S. COBB, AND N. MARSHALL. 1968. Size compositions of inshore and offshore larvae of the lobster, *Homarus americanus*, off southern New England. Proc. Natl. Shellfish. Assoc. 58: 78–81.

SAILA, S. B., AND J. M. FLOWERS. 1968. Movements and behavior of berried female lobsters displaced from offshore areas to Narragansett Bay, Rhode Island. J. Cons. Perm. Int. Explor. Mer 31: 342–351.

SASAKI, G. C., J. M. CAPUZZO, AND P. BIESIOT. 1986. Nutritional and bioenergetic considerations in the development of the American lobster *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2311–2319.

SASTRY, A. N. 1980. Effects of thermal pollution on pelagic larvae of Crustacea. Environ. Prot. Agency (U.S.) Tech. Rep. EPA-600/3-80-064: 52 p.

SASTRY, A. N., AND D. C. MILLER. 1981. Application of biochemical and physiological responses to water quality monitoring, p. 265–294. *In* J. Vernberg, A. Calabrese, F. P. Thurberg, and W. B. Vernberg [ed.] Biological monitoring of marine pollutants. Academic Press, New York, NY.

SASTRY, A. N., AND J. A. PECHENIK. 1977. A review of ecology, physiology and behavior of lobster larvae (*H. americanus* and *H. gammarus*). CSIRO Div. Fish. Oceanog. (Aust.) Circ. 7: 159–173.

SASTRY, A. N., AND S. L. VARGO. 1977. Variations in the physiological responses of crustacean larvae to temperature, p. 401–423. *In* F. J. Vernberg, A. Calabrese, F. P. Therberg, and W. B. Vernberg [ed.] Physiological responses of marine biota to pollutants. Academic Press, New York, NY.

SCARRATT, D. J. 1964. Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. J. Fish. Res. Board Can. 21: 661–680.

1968. An artificial reef for lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 25: 2683–2690.

1973. The effects of raking Irish moss (*Chrondrus crispus*) on lobsters in Prince Edward Island. Helgol. Wiss. Meeresunters. 24: 415–424.

1974. Impact of spills and clean-up technology on living animal resources, and resource based industry. Fish. Res. Board Can. Tech. Rep. 428: 141–158.

SCARRATT, D. J., AND G. E. RAINE. 1967. Avoidance of low salinity by newly hatched lobster larvae. J. Fish. Res. Board Can. 24: 1403–1406.

SHEEHY, D. J. 1976. Utilization of artificial shelters by the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 33: 1615–1622.

SINDERMANN, C. J. 1977. Lobster diseases, p. 152–183. *In* C. J. Sindermann [ed.] Developments in aquaculture and fisheries science. Vol 6. Disease diagnosis and control in North American aquaculture. Elsevier Scientific Publishing Co., Amsterdam, The Netherlands.

SMITH, E. M. 1977. Some aspects of catch/effort, biology, and the economics of the Long Island sound lobster fishery during 1976. Final Report, USDC, NMFS, Connecticut, Project No. 3-253-R-1: 97 p.

SMOLOWITZ, R. J., AND F. M. SERCHUK. 1980. Recent U.S. lobster trap gear research: applications and implications. Can. Tech. Rep. Fish. Aquat. Sci. 932: 73–76.

SPRAGUE, J. B., AND D. W. MCLEESE. 1968. Toxicity of kraft pulp mill effluent for larval and adult lobsters, and juvenile salmon. Water Res. 2: 753–760.

SQUIRES, H. J. 1970. Lobster (*Homarus americanus*) fishery and ecology in Port au Port Bay, Newfoundland, 1960–65. Proc. Natl. Shellfish. Assoc. 60: 22–39.

SQUIRES, H. J., G. E. TUCKER, AND G. P. ENNIS. 1971. Lobsters (*Homarus americanus*) in Bay of Islands, Newfoundland, 1963–65. Fish. Res. Board Can. Tech. Rep. 1151: 58 p.

STASKO, A. 1978. Inshore–offshore SW Nova Scotia lobster stock interaction: a hypothesis. CAFSAC Res. Doc. 78/37. (Available from Library, Biological Station, St. Andrews, N.B. E0G 2X0)

STEWART, J. E. 1978. The lobster disease, gaffkemia, in relation to fisheries management. Int. Counc. Explor. Sea C.M. 1978/F:16.

1980. Diseases, p. 301–342. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

1984. Lobster diseases. Helgol. Wiss. Meeresunters. 37: 243–254.

TEMPLEMAN, W. 1936a. Local differences in the life history of the lobster (*Homarus americanus*) on the coast of the Maritime provinces of Canada. J. Biol. Board Can. 2: 41–87.

1936b. Fourth stage larvae of *Homarus americanus* intermediate in form between normal third and fourth stages. J. Biol. Board Can. 2: 349–354.

1936c. The influence of temperature, salinity, light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J. Biol. Board Can. 2: 485–497.

1939. Investigations into the life history of the lobster (*Homarus*

*americanus*) off the coast of Newfoundland, 1938. Nfld. Dep. Nat. Res. Res. Bull. (Fish.) 7: 52 p.

1940a. Embryonic development rates and egg-laying of the Canadian lobster. J. Fish. Res. Board Can. 5: 71–83.

1940b. The life history of the lobster. Nfld. Dep. Nat. Res. Serv. Bull. 15: 42 p.

1948. Growth per moult in the American lobster. Bull. Nfld. Gov. Lab. 18: 26–48.

THOMAS, M. L. H., AND G. N. WHITE. 1969. Mass mortality of estuarine fauna at Bideford, P.E.I., associated with abnormally low salinities. J. Fish. Res. Board Can. 26: 701–704.

THORSON, G. 1950. Reproduction and larval ecology of marine bottom invertebrates. Biol. Rev. Cambridge Philos. Soc. 25: 1–45.

THURBERG, F. P., A. CALABRESE, E. GOULD, R. A. GREIG, M. A. DAWSON, AND R. K. TUCKER. 1977. Response of the lobster, *Homarus americanus*, to sublethal levels of cadmium and mercury, p. 185–197. *In* F. J. Vernberg, A. Calabrese, F. P. Thurberg, and W. B. Vernberg [ed.] Physiological responses of marine biota to pollutants. Academic Press, New York, NY.

UHAZY, L. S., D. E. AIKEN, AND A. CAMPBELL. 1985. Morphology and systematics of the nemertean *Pseudocarcinonemertes homari* (Hoplonemertea: monostilifera) from the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 342–350.

UZMANN, J. R., R. A. COOPER, AND K. J. PECCI. 1977. Migration and dispersion of tagged American lobsters, *Homarus americanus*, on the southern New England continental shelf. NOAA Tech. Rep. NMFS SSRF-705: 92 p.

WADDY, S. L., AND D. E. AIKEN. 1984a. Absence of photoperiodic control over time of spawning in the American lobster. Am. Zool. 24: 143A.

1984b. Seed stock for lobster culture: the role of temperature in synchronizing the molt and reproductive cycle of cultured American lobsters. J. World Maricult. Soc. 15: 132–137.

1984c. Broodstock management for year-round production of larvae for culture of the American lobster. Can. Tech. Rep. Fish. Aquat. Sci. 1272: 14 p.

1984d. Environmental regulation of ovarian development in the American lobster, p. 649. *In* W. Engels, W. H. Clark, Jr., A. Fischer, P. J. W. Olive, and D. F. Went [ed.] Advances in invertebrate reproduction 3. Elsevier Science Publishers, Amsterdam, The Netherlands.

1985. Immunofluorescent localization of American lobster egg yolk protein in the alimentary tract of the nemertean *Pseudocarcinonemertes homari*. Can. J. Fish. Aquat. Sci. 42: 357–359.

WICKHAM, D. E. 1979. *Carcinonemertes errans* and the fouling and mortality of eggs of the Dungeness crab, *Cancer magister*. J. Fish. Res. Board Can. 36: 1319–1324.

1980. Aspects of the life history of *Carcinonemertes errans* (Nemertea: Carcinonemertidae), an egg predator of the crab *Cancer magister*. Biol. Bull. 159: 247–257.

1986. Epizootic infestations by nemertean brood parasites on commercially important crustaceans. Can. J. Fish. Aquat. Sci. 43: 2295–2302.

WILDER, D. G. 1953. The growth rate of the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 10: 371–412.

1965. Lobster conservation in Canada. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 156: 21–29.

YOUNG, J. S., AND J. B. PEARCE. 1975. Shell disease in crabs and lobsters from New York Bight. Mar. Pollut. Bull. 6: 101–105.

# Crustacean Endocrinology, A Review

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Crustacean endocrinology has benefited from the recent advances in peptide chemistry and immunoassay. Current research has focused on the isolation of peptides and the measurement of steroids. Terpenoid hormones, long known from insects, are now believed to be present and active in crustaceans. The role of biogenic amines as neuromodulators and neurohormones in crustaceans is also being examined. Details of crustacean regulatory physiology suggest a similarity to well-known insect patterns. This brief review will examine some examples from each of these areas.

L'endocrinologie des crustacés a tiré profit des progrès récemment obtenus dans les domaines de la chimie des peptides et des tests immunologiques. La recherche actuelle est axée sur l'isolation des peptides et la mesure des stéroïdes. Les hormones terpénoïdes, connues depuis longtemps chez les insectes, semblent maintenant être présentes et actives chez les crustacés. On examine également le rôle des amines biogènes en tant que neuromodulateurs et neurohormones chez les crustacés. Le détail de la physiologie de la régulation chez les crustacés semble présenter des ressemblances avec certains phénomènes bien connus chez les insectes. Cette brève étude puisera quelques exemples dans chacun de ces domaines.

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The objective of this review was to assemble the recent literature of crustacean endocrinology and present it in a summary format. I have generalized recent advances and research directions and have indicated gaps in the available knowledge. I hope that this brief review will provide both the general reader and the comparative endocrinologist an update on crustacean endocrinology. The diversity of published research prevents a detailed analysis of any particular topic, so where available, detailed review articles were cited.

Four classes of compounds are implicated as endocrine messengers which may regulate arthropod physiology: biogenic amines, peptides, steroids, and terpenoids. Traditionally, endocrines were thought to have an action at a distance, travelling through the haemolymph to a target tissue. It is now evident that several peptides, which fit classical definitions of hormones, have localized actions on target neurons or neurosecretory cells (Hokfelt et al. 1980; Quackenbush and Fingerman 1984a, 1984b). Additionally, peptide hormones are produced and released from neurons which also produce classical neurotransmitters, such as biogenic amines (Lundberg and Hokfelt 1983; Kravitz et al. 1983). Biogenic amines, initially identified as neurotransmitters, also circulate naturally in crustacean haemolymph at levels high enough to act as neurohormones or neuromodulators (Cooke and Sullivan 1982; Kravitz et al. 1983; Kupfermann 1979 for review).

One interesting and common thread through all investigations of comparative endocrinology is the presence of the same types of hormones in protostomes and in deuterostomes. Terpenoids remain unique to arthropods. By contrast, the biosynthesis, release, and mode of action of the peptides and biogenic amines are, in the broad view, the same in arthropods and vertebrates.

Ecdysone is the most studied steroid of arthropods. It is found also in plants, cestodes, trematodes, and nematodes (Hanaoka and Hagadorn 1980; Skinner 1985a, 1985b; Whitehead 1983). Crustaceans obtain cholesterol, the precursor to ecdysone, from their diet. They subsequently modify cholesterol to the hormone. The most active site for ecdysone synthesis and release in crustaceans is the Y-organ (Birkenbeil and Eckert 1983; Skinner 1985a; Soumoff and O'Connor 1982). Like most steroid hormones, ecdysone binds to a nuclear receptor and then affects either translation or transcription or both (Koolman and Spindler 1983; Londershausen and Spindler 1985; Raabe 1982; Spindler et al. 1980). The pattern of ecdysone release during the molt cycle is basically the same in crustaceans and insects, with some modifications. Initially, a small amount of ecdysone (10–50 ng/mL haemolymph) is released prior to apolysis. A second larger release of ecdysone (150–350 ng/mL haemolymph) occurs later in the molt cycle. Just before actual ecdysis, the haemolymph levels of ecdysone drop rapidly (Chang 1984; Chang and Bruce 1980; Hopkins 1983; Skinner 1985b). The release of ecdysteroid from the Y-organ and its action at epidermal tissue is affected by peptide factors from the eyestalk (Freeman 1980; Freeman and Costlow 1979; Soumoff and Skinner 1980).

The neuroendocrine system of stalk-eyed crustaceans has been studied for several decades (Fingerman 1985 for review). A group of neurosecretory cells in the eyestalk comprise the X-organ. These cells send the majority of their axons to a

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TABLE 1. Peptides extracted from whole eyestalks or sinus glands of crustacean tissues. Peptide names are described in the text. A plus sign indicates known amino acid composition for that peptide.

| Name | Molecular size (daltons) | Sequence | Amino acid | Action | Reference |
|---|---|---|---|---|---|
| RPCH (PCH) | 970 | Yes | + | Pigments | Josefsson 1983 |
| DRLAH (PDH) | 1800 | Yes | + | Pigments | Josefsson 1983a |
| CHH (HGH) | 5000–7000 | No | + | Sugar | Keller et al. 1985 |
| NDH | 1200 | No | − | Nerves | Arechiga et al. 1985 |
| GIH | 2000–5000 | No | − | Gonads | Charniaux-Cotton 1985 |
| MIH | 1000–5000 | No | − | Molt | Chang 1985 |
| BPDH | 1387 | No | + | Pigment | Quackenbush and Fingerman 1985 |
| LGIF | 1000 | No | − | Limb bud | Hopkins et al. 1979 |

TABLE 2. Peptides localized in crustacean tissues. RIA = radioimmunoassay; histology = immunocytochemistry using specific antibodies; isolated = isolated using chromatography and compared with the native peptide for identification; ? = no information.

| Name | Source | Method | Action | References |
|---|---|---|---|---|
| Insulinlike | Hepatopancreas | RIA | Vitellogenesis | Sanders 1983a, 1983b, 1983c |
| Proctolinlike | Pericardial organ | RIA/isolated | Muscle | Sullivan 1979 |
| Gastrin/CCK-like | Stomach | Histology/isolated | ? | Larson and Vigna 1983a, 1983b |
| Vassopressinlike | Eyestalk | Histology | ? | VanHerp and Bellon-Humbert 1982 |
| Neurophysinlike | Eyestalk | Histology | ? | VanHerp and Bellon-Humbert 1982 |
| Enkephalinlike | Eyestalk | Histology/physiology | Peptide release | Mancillias et al. 1981; Fingerman 1985 |
| Substance-P-like | Eyestalk | Histology | ? | Fingerman et al. 1985 |
| Somatostatinlike | Brain | Histology | ? | Martin and Dubois 1981 |
| FMRF-like | Eyestalk | Histology | ? | Fingerman et al. 1985 |

neurohaemal organ, called the sinus gland. This neuroendrocine system lies within the major eyestalk ganglia (Cooke and Sullivan 1982; Arsenault 1981). This system produces factors which affect crustacean homeostasis (Table 1), and it is also a site for sensory integration (Ache and MacMillian 1980). Virtually all aspects of crustacean physiology are affected by eyestalk removal. The best understood products of this system are the chromatophorotropins, small peptides which regulate pigment translocation in epidermal and retinal cells (Fingerman 1985; Rao and Fingerman 1983). Several other endocrine factors are attributed to the eyestalk neuroendocrine system (Table 1). Other sites of peptide hormone synthesis and release include the pericardial organs, postcommissural organs, and thoracic ganglion (Table 2). In addition, immunocytochemical techniques identify the presence of vertebrate peptide hormones in the eyestalk, hepatopancreas, and stomach of crustaceans (Table 2). The role of these naturalized peptides remains to be elucidated (Greenberg and Price 1983).

Terpenoid hormones have been studied in insects, but only recently have they been found in the haemolymph of crustaceans (Berreur-Bonnenfant and Lawrence 1984; Ferezou and Barbier 1978; Laufer et al. 1984, 1985) (Table 3). Terpenoids are simple lipoidal compounds; the isoprene molecule is the basic structural unit. In crustaceans, terpenoids are found in the androgenic gland and mandibular organ. Farnesylacetone, an androgenic hormone, affects gonadal growth in male and female crabs (Berreur-Bonnenfant and Lawrence 1984). Methylfarnesoate, produced in the mandibular organ and found in the haemolymph, may be the crustacean analog of insect juvenile hormone (Laufer et al. 1984, 1985). A full understanding of the role of terpenoids in crustanceans may help to explain some long-standing controversies concerning regulation of molting and of reproduction (Charniaux-Cotton 1985; Skinner 1985a).

## Ecdysteroid Control of Molting

The details of ecdysteroid control of crustacean molting are being elucidated, in part due to the increased resolution of current radioimmunoassays (Aiken 1980; Chang 1984, 1985; Charmantier 1980; Hopkins 1986; O'Connor 1985; Skinner 1985a, 1985b). Initial observations found that haemolymph ecdysteroid titers reached a maximum just before ecdysis and then fell to resting levels at ecdysis (stage E) (Chang et al. 1976). This crustacean pattern seemed less complex and different from insect patterns which showed several carefully timed elevations of ecdysteroids in haemolymph (Downer and Laufer 1983; Raabe 1982). However, recent results show resemblances between the crustacean and insect patterns of ecdysteroid secretion (Aiken 1980; Baldaia et al. 1984; Hopkins 1983; Skinner 1985a; 1985b; Stevenson et al. 1979). In general, at retraction of the epidermis a small ecdysteroid peak is observed, called peak 1 (Hopkins 1983, 1986) (Fig. 1). Peak 1 may go undetected in some assays and may be delayed until stage $D_1$ (Chang 1984; Hopkins 1983; Stevenson et al. 1979). Subsequently, a much larger second peak of ecdysteroid called peak 2 is released just prior to ecdysis (Hopkins 1983). Peak 2 is measured more often in crustaceans than peak 1 (Skinner 1985a). The total amount of circulating ecdysteroid appears variable among crustaceans. For example, crabs release much less ecdysteroid than homarid lobsters (Chang 1984, 1985; Hopkins 1983) (Fig. 1). This difference may be due to measurement techniques or to species differences.

TABLE 3. Steroids and terpenoids in crustaceans. RIA = radioimmunoassay; HPLC = high pressure liquid chromatography; GC-MS = gas chromatography – mass spectroscopy; isolated = isolation and comparison with known compounds; H-P and L-P = unidentified high and low polar steroid, respectively, extracted from Y-organ.

| Name | Source | Method | Action | References |
|---|---|---|---|---|
| Ecdysone | Y-organ/ovary | RIA/HPLC | Molt | Chang 1985 |
| 20-OH-E | Y-organ/carcass | RIA | Molt | Hopkins 1983, 1986 |
| H-P steroid | Y-organ | HPLC/RIA | Molt ? | Hopkins 1986 |
| L-P steroid | Y-organ | HPLC/RIA | Molt ? | Hopkins 1986 |
| Farnesylacetone | Androgenic gland | Isolated/GC-MS | Inhibits gonad | Ferezou and Barbier 1978 |
| JH III-like | Mandibular organ | Isolated/GC-MS | ? | Laufer et al. 1985 |
| Progesterone | Ovary | RIA | ? | Couch et al. 1978 |

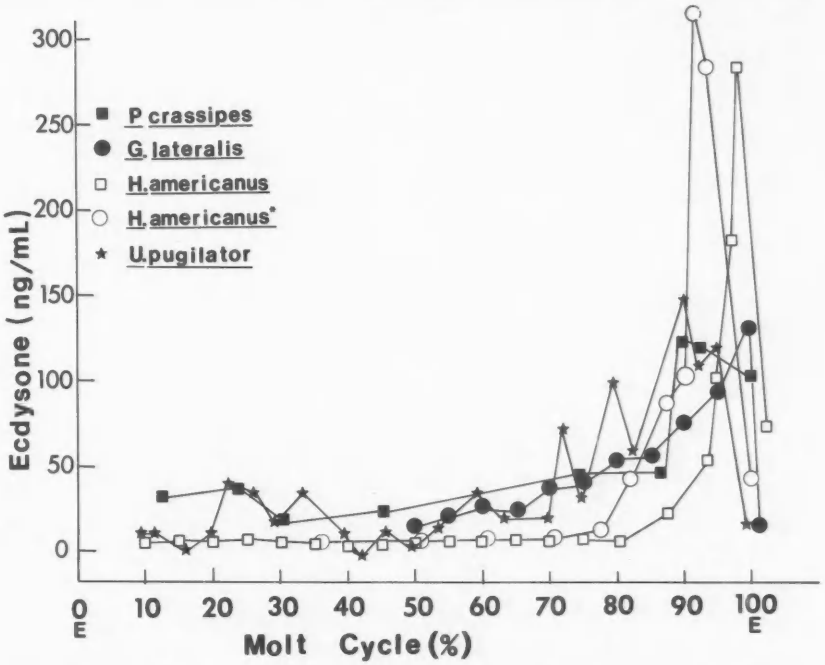


FIG. 1. Ecdysone levels in the haemolymph of several crustaceans during the molt cycle. The duration of the molt cycle (from ecdysis to ecdysis) varies in each species. Durations (in days) were all normalized to 100% (ecdysis to ecdysis) for comparative purposes. Data: *P. crassipes* from O'Connor (1985); *G. lateralis* from Skinner (1985a); *H. americanus* (□) adult from Chang (1984); *H. americanus* (○) subadult from Chang and Bruce (1980); *U. pugilator* from Hopkins (1983). See references for details of ecdysone radioimmunoassays.

Ecdysteroid release varies over the molt cycle and so does the composition of the ecdysteroids in the haemolymph (Baldaia et al. 1984; Hopkins 1983, 1986). The early stages of the molt cycle have a 1:1 or 1:2 ratio of α-ecdysone to β-ecdysone. As the cycle progresses, the ratio changes to 1:4 or greater (Baldaia et al. 1984; Hopkins 1986). This change from equal to different levels of α- and β-ecdysone is also found in insects (Bollenbacher et al. 1975; Koolman and Spindler 1983). The changing pattern and composition of haemolymph ecdysteroids cannot be explained as yet, but these data underscore the complexity of the system.

The ecdysteroids of entire first-stage larval lobsters vary over the molt cycle (Chang and Bruce 1981). A single broad peak of ecdysteroid was found in the middle of the molt cycle of the first three larval molts. Larval crustaceans appear to possess both rudimentary Y-organs and X-organs (Arsenault 1981; McConaugha 1980). Therefore, it is possible that larval crustaceans use the same endocrines as adults to control molting. Both larval and adult insect molting is regulated by ecdysteroids (Raabe 1982). Exogenous ecdysteroids induce molting in larval horseshoe crabs, probably mimicing natural events. A sensitive bioassay for ecdysteroids was developed based on the effect of exogenous ecdysteroids on the molt cycle of these horseshoe crab larvae (Jegla 1982; Jegla and Costlow 1979). A functioning ecdysteroid control system is apparently developed early in the life of arthropods.

Regulation of haemolymph ecdysteroid levels can be affected through several common pathways. Studies of the Y-organ in vitro have shown that either partially purified or crude eyestalk extracts can slow or stop natural release of

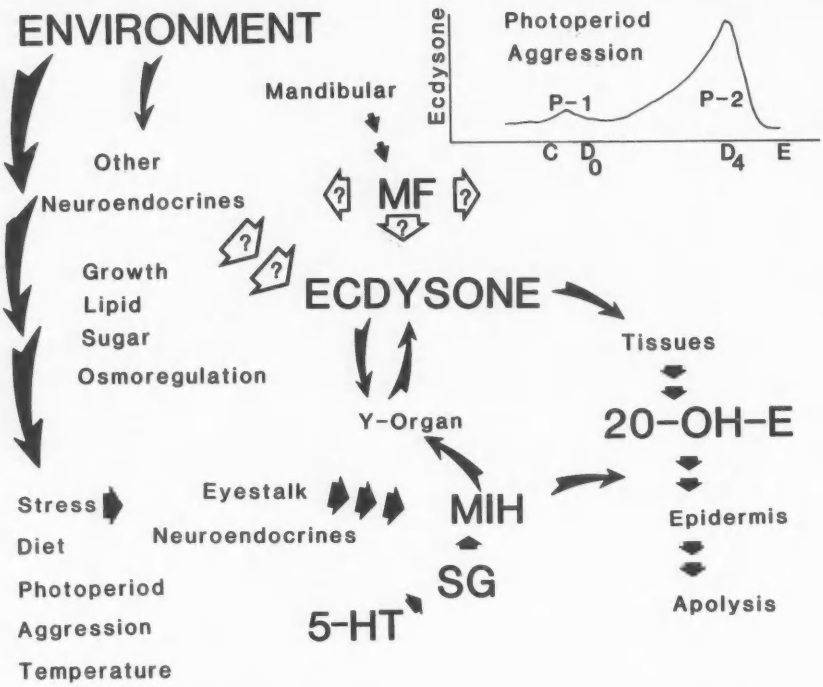


FIG. 2. Factors affecting the molt cycle, and associated endocrines from crustaceans. 5-HT = serotonin, SG = sinus gland, MIH = molt inhibiting hormone, 20-OH-E = 20-hydroxy-ecdysone MF = methyl-farnesoate. Pathways and interactions are detailed in the text. The inset summarizes when photoperiod and aggression can affect the molt cycle, using the traditional molt stages (Aiken 1980).

ecdysteroids (Hopkins 1983, 1986; Mattson and Spaziani 1985b; Soumoff and O'Connor 1982). Molt inhibiting hormone (MIH) may also act on the target tissues of ecdysteroids directly blocking the effects of ecdysteroids (Freeman 1980; Freeman and Costlow 1979). Ecdysteroids may also regulate their own production through a direct feedback on the Y-organ (Hopkins 1986). In addition, several external environmental factors affect the molt cycle directly (for review see Aiken 1980; Skinner 1985a, 1985b). For example, Mattson and Spaziani (1985a, 1985b) found that stress from handling lowers ecdysteroid levels in crabs, perhaps enough to slow the molt cycle. Limb loss, natural or contrived, usually accelerates the molt cycle, and the acceleration is mediated by ecdysteroid systems (Hopkins et al. 1979; Skinner 1985b for review). However, crustaceans may molt without measurable growth, which suggests an unknown control for growth (Aiken 1980; Hopkins 1982; Skinner 1985a).

Crustaceans have ecdysteroids in several tissues other than the Y-organ (Baldaia et al. 1984; Chang 1978, 1984, 1985; Spindler et al. 1980). The function of these ecdysteroids is not known. Ecdysteroids control vitellogenesis in some insects, but appear to have no effect in other insect species (Briers and Huybrechts 1984; De Loof et al. 1984; Hanaoka and Hagadorn 1980). It was suggested that ecdysteroids regulate some aspects of crustacean reproduction, since they have been found in gonads of several species (Adiyodi and Subramoniam 1983; Chang 1978; Lachaise and Hoffmann 1977). Exogenous ecdysone and 20-hydroxy-ecdysone (20-OH-E) stimulated vitellogenesis in isolated ovaries of the isopod *Porcellio dilatatus* (Gohar and Souty 1984) but inhibited vitellogenesis in cirripedes (Fyhn et al. 1977). Ovarian-produced ecdysteroids are required for full vitellogenesis in the amphipod *Orchestia gammarella* (Blanchet-Tournier 1982).

## Peptide Hormones of Crustacea

The first fully defined crustacean peptide hormone was red pigment concentrating hormone (RPCH), beginning a new era in crustacean research (Fernlund and Josefsson 1972; Josefsson 1983a, 1983b). RPCH was the first definitive example of a new class of peptides unique to invertebrates (Greenberg and Price 1983). Investigations on products from the eyestalk neuroendocrine system have proceeded along several fronts, some of which will be summarized in this review (see Arechiga et al. 1985; Cooke and Sullivan 1982; Fingerman 1985; Newcomb et al. 1985 for reviews).

The location of the eyestalk neuroendocrine system makes it amenable to laboratory investigations. Regulation by eyestalk factors or hormones has been proposed for many physiological processes (Cooke and Sullivan 1982). However, even the X-organ – sinus gland complex is composed of a limited number of cells (Arsenault 1981 for review). Processing within the eyestalk of large precursor peptides to smaller peptides which eventually circulate in the haemolymph could account for the diversity of endocrine factors attributed to the eyestalk (Newcomb 1983; Newcomb et al. 1985; Stuenkel 1983). Other neuroendocrine centers have received less attention. For example, pericardial organs, located next to the heart, contain

peptides and biogenic amines which are involved in endocrine regulation (Cooke and Sullivan 1982; Sullivan 1979; Sullivan et al. 1976).

### Chromatophorotropins

Epidermal chromatophores and retinal pigments of crustaceans are controlled by pairs of peptides which have antagonistic actions (Fingerman 1985; Rao 1985; Rao and Fingerman 1983). Dispersion and concentration of the pigment granules within the epidermal and retinal cells are affected by eyestalk peptides. Red chromatophores (erythrophores) of shrimp served as the bioassay for RPCH (Fernlund and Josefsson 1972). Subsequently, it was found that RPCH also affected black and white chromatophores and thus was renamed pigment concentrating hormone (PCH) (Josefsson 1983a, 1983b). Likewise, distal retinal light adapting hormone was renamed pigment dispersing hormone (PDH) when it was found also to affect epidermal chromatophores (Josefsson 1983a). These two peptides could account for pigment dispersion and concentration within epidermal chromatophores. However, both PDH and PCH affect different chromatophores equally; these are totipotent peptides. Thus, in the presence of PCH or PDH, different chromatophores (melanophores and erythrophores) have the same state of pigment dispersion. Intact, living crabs generally have the pigments within the chromatophores in different states of dispersion. Totipotent peptides cannot produce the different stages of dispersion observed in live crabs (Fingerman 1985; Quackenbush and Fingerman 1984a; Riehm and Rao 1982). Peptides with a singular action on a specific type of chromatophore can also be released from the crab eyestalk neuroendocrine system (Fingerman 1985 for review). For example, black pigment dispersing hormone (BPDH) is released from the isolated crab eyestalk. BPDH was also found in the haemolymph of crabs with dispersed black pigment (Quackenbush and Fingerman 1984a, 1984b, 1984c, 1985) (Table 1). BPDH, which only affects melanophores, is distinct from PDH although it shares a similar amino acid composition (Josefsson 1983a; Quackenbush and Fingerman 1984c) (Table 1). The differences between the totipotent peptides PDH and PCH and the specific peptide BPDH remain to be resolved. Measurement of circulating levels of these peptides would clarify the present apparent conflict.

Why crustaceans possess such a complex and elegant system for controlling color remains unclear. It was traditionally accepted that the ability to change color would benefit crustaceans in thermoregulation and by protection from damage from ultraviolet light (Fingerman 1963). Body coloration may be an indicator of reproductive readiness or competence in adult crabs (Quackenbush and Herrnkind 1983b; Zucker 1980, 1984). Exercise brings about a color change in crabs which is affected by an eyestalk factor (Herreid and Mooney 1984). The role of chromatophorotropins may not be limited to control of chromatophores. RPCH is a cardioexcitor in molluscs (Greenberg et al. 1985). RPCH was found in the eyestalk of adult *Homarus americanus*, which do not change color with chromatophores (Jaffe et al. 1984).

### Peptides Affecting the Molt Cycle

Zeleny reported in 1905 that eyestalk ablation shortens the crustacean molt cycle. Since that initial finding, the elusive MIH has been sought with variable results (Chang 1985; Skinner 1985a, 1985b; Zeleny 1905) (Tables 1 and 4). Progress in the isolation of MIH has been slow due to the lack of a generally accepted bioassay (Bruce and Chang 1984; Freeman and Costlow 1979; Quackenbush and Herrnkind 1983a, 1983b; Rao 1965; Soyez and Kleinholz 1977). Radioimmunoassay for ecdysteroids from haemolymph or Y-organ cultures provides a useful indirect assay for MIH (Bruce and Chang 1984; Soumoff and O'Connor 1982). MIH blocks ecdysteroid release from the Y-organ and the action of ecdysteroid at the target tissues (Freeman 1980; Freeman and Costlow 1979; Hopkins 1983, 1985; Soumoff and Skinner 1980). The products of the eyestalk system affect molt cycle duration early in the molt cycle; ablation has no effect in the later stages of the molt cycle. MIH does not affect the later stages of the ecdysteroid patterns (Hopkins 1983; Skinner 1985a). Shortening the transition from intermolt to premolt was the most significant effect of eyestalk ablation in spiny lobsters (Quackenbush and Herrnkind 1981, 1983a). It is this transition state that was most affected by changes in the photoperiod as well (Quackenbush and Herrnkind 1983a). Dramatic changes in the aggressive behavior of homarid lobsters have also been documented during this transition stage (Tamm and Cobb 1978). Stress from handling can lower the ecdysteroid level in the haemolymph dramatically, and this response is mediated by MIH from the eyestalk (Mattson and Spaziani 1985a, 1985b). Environmental factors have a direct access to the endocrine system. Photoperiod and temperature could control molting through MIH regulation of ecdysteroid release or target tissue response (Fig. 2).

### Peptides Affecting Reproduction

Crustaceans can regulate gonadal and somatic growth to achieve an optimum balance between the two processes. Most crustaceans can be placed into one of three groups based on the organization of these two processes (Adiyodi and Subramoniam 1983; Charniaux-Cotton 1985) (Fig. 3). Crabs and lobsters fit into type 1 where reproduction takes place during the relatively long intermolt period. Isopods, amphipods, and some shrimps fit into type 2 where gonadal and somatic growth occur simultaneously. Type 3 includes the rapid molting cirripedes where reproduction may require several molt cycles. These groupings describe extremes because many species fit between two of these general groups. Even using these simplified groups to describe the relationships of molting and reproduction, the endocrine control mechanisms that generate the observed patterns are complex. Since crustaceans produce yolky eggs, reproduction requires significant energy that is partitioned into two phases (Fig. 4). Vitellogenin, the precursor of the yolk protein vitellin, can be produced in the hepatopancreas or the ovary (Charniaux-Cotton 1985 for review). In crustaceans, during primary vitellogenesis, the ovary manufactures yolk with slight increase in gonad size. Secondary vitellogenesis is characterized by a massive increase in vitellogenesis and increase in gonad weight, with yolk coming from both endogenous (gonad) and exogenous (hepatopancreas) sources (Charniaux-Cotton 1985; Blanchet-Tournier 1982). The role and contribution of exogenous vitellogenesis varies from species to species, and not all crustaceans require exogenous vitellin (Adiyodi and Subramoniam 1983; Dehn et al. 1983).

Crustacean reproduction is affected by steroids and peptides. The role of ecdysone is well established in insects, where it is

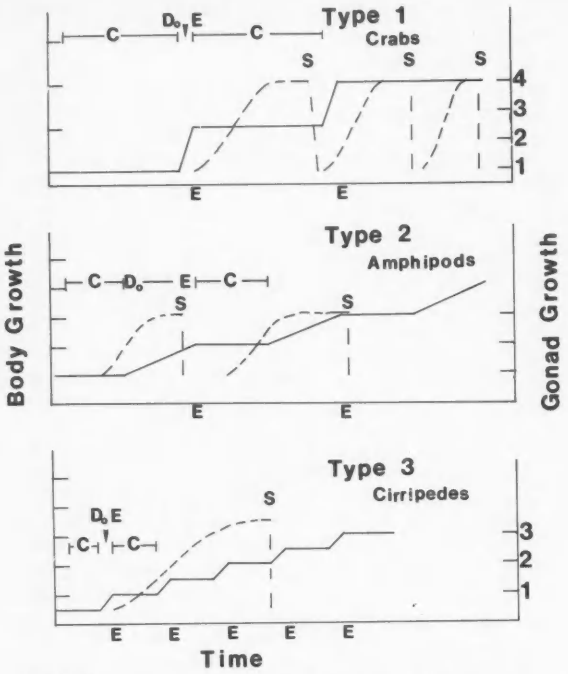


FIG. 3. Interactions of somatic and gonadal growth of female crustaceans. Classification scheme taken from Adiyodi and Subramoniam (1983). Growth is in arbitrary units. Spawning occurs at S. The molt cycle is divided into the stages intermolt (C) and proecdysis ($D_0$ to E). Type 1 are crabs and lobsters, type 2 are isopods, amphipods, and some shrimps, and type 3 are cirripedes. Solid line = somatic growth; broken line = gonadal growth.

required for vitellogenesis in several species (De Loof et al. 1984; Hanaoka and Hagadorn 1980). In amphipods, ecdysone is produced in the ovary, and ecdysone is required for vitellogenesis (Blanchet-Tournier 1982; Charniaux-Cotton 1985) Fig. 5). In decapods, ecdysteroids are found in gonad tissue, yet no role for steroids in regulation of reproduction is documented. The hormones and pathways for control of reproduction of a mosquito and an amphipod, *O. gammarella*, are diagrammed in Fig. 5. These models clearly do not hold for all insects nor for all crustaceans, but they show how closely related the systems may be (Blanchet-Tournier 1982; De Loof et al. 1984; Hanaoka and Hagadorn 1980)

Neuroendocrine control of vitellogenesis in shrimps and crabs was first demonstrated by eyestalk ablation experiments showing stimulation of secondary vitellogenesis (Bomirski and Klek 1974; Brown and Jones 1948; Panouse 1943). A gonad inhibiting hormone (GIH) was postulated, and three attempts at isolation have provided three different molecular sizes for GIH (2000, 5000, >5000) (Charniaux-Cotton 1985; Bomirski et al. 1981; Quackenbush and Herrnkind 1983b). Implantantion of thoracic ganglions or their extracts stimulated gonad growth in several crustaceans. Based on these observations, a gonad stimulation hormone (GSH) was also postulated, but not yet isolated (Eastman-Reks and Fingerman 1984; Hinsch and Bennett 1979; Otsu and Hanaoka 1951). Complex models for the control of reproduction have been devised using data from several sources (Fig. 5). The best developed crustacean model

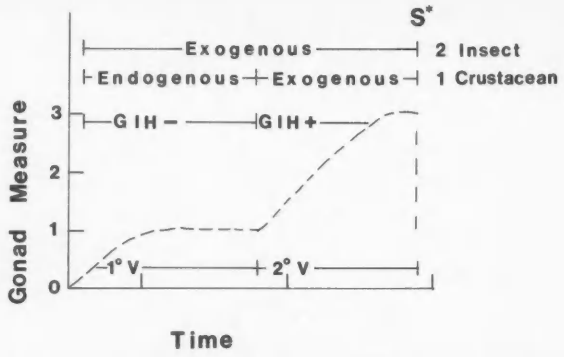


FIG. 4. Stages of vitellogenesis in Crustacea. This diagram is based on data summarized in Charniaux-Cotton (1985) and Adiyodi and Subramoniam (1983). Primary vitellogenesis (1° V) and secondary vitellogenesis (2° V) precede spawning (S*). Plan 1 had endogenous and exogenous sources of vitellogenin, a crustacean type. Plan 2 has only an exogenous source of vitellogenins, an insect type. Gonad inhibiting hormone (GIH) affects secondary vitellogenesis (GIH+). GIH has no effect on primary vitellogenesis (GIH−). Note that after spawning, most crustaceans restart the process at secondary vitellogenesis.

is for the amphipod *O. gammarella*. This and the model proposed for insects provide a guide for future research in this area.

## Crustacean Hyperglycemic Hormone

Crustaceans regulate their haemolymph sugar, primarily glucose, with crustacean hyperglycemic hormone (CHH) (Keller 1983; Keller and Kegal 1984; Keller et al. 1985; Kleinholz and Keller 1979). During the molt cycle, haemolymph sugar rises, falling to resting levels after ecdysis (Telford 1968a). Handling crustaceans also increases haemolymph sugar, and stressed lobsters in commercial ponds have elevated haemolymph sugar compared with wild animals (Telford 1968b). Injections of purified CHH elevate sugar levels in 5−10 min, lasting for 2 h. So, stress-induced sugar elevations from quick handling may be a result of CHH release (Keller et al. 1985; Keller and Andrew 1973). The hepatopancreas and abdominal muscles are target tissues for CHH (Sedlmeier 1985). Isolation of pure CHH from either whole eyestalks or isolated sinus glands has been achieved in several crustacean species (Keller and Kegal 1984; Martin et al. 1984a, 1984b). CHH is unique among crustacean peptides in that it has group specificity. For example, CHH from crab sources has little effect on crayfish and vice versa (Keller et al. 1985). Two research groups have produced antibodies to CHH and reported that the X-organ − sinus gland complex is the major source of CHH (Gorgels-Kallen and VanHerp 1981; Jaros and Keller 1979). Preliminary results show that CHH is found in the haemolymph; resting levels are estimated to be 180 fmol/mL (Keller et al. 1985). Injections of the neurotransmitter serotonin (5-HT) induce hyperglycemia in intact crayfish but not in eyestalk ablated animals. This suggests that 5-HT may release CHH from the sinus gland (Keller and Beyer 1968).

## Neurodepressing Hormone

Neurodepressing hormone (NDH) is a small (1200 dalton) peptide which has a direct action on nerve cells (Arechiga et al.

1985 for review) (Table 2). One effect of eyestalk ablation is a quantitative and qualitative change in the circadian locomotory activity (Arechiga et al. 1980). It was postulated that the eyestalk contained a factor which depresses general activity; this factor was subsequently isolated and characterized (Huberman et al. 1979). NDH has a direct action on different types of nerve cells from several species (Arechiga et al. 1979a, 1979b). Perfusion of spontaneously active nerve cells with NDH results in an immediate cessation of electrical activity. NDH has been found in the haemolymph, and it has a long residence time (Arechiga and Huberman 1980; Arechiga et al. 1979a). The neurotransmitter γ-aminobutyric acid (GABA) can inhibit the release of NDH from isolated neuroendocrine tissues (Arechiga et al. 1985). Cyclic changes in eyestalk content of NDH suggest that NDH regulates circadian activity in crustaceans (Arechiga et al. 1985).

### Limb Growth Inhibiting Factor

Limb growth inhibiting factor (LGIF) isolated from eyestalk tissue was thought to be different from MIH (Bliss and Hopkins 1973; Hopkins et al. 1979). LGIF has some characteristics of MIH, but it was distinquished from MIH based on the difference in molecular size estimated from column chromatography (Hopkins et al. 1979). LGIF inhibits rapid proecdysial growth of limbs which occurs early in the molt cycle. Limb buds were not affected by LGIF during the later stages of the molt cycle. Since the size of MIH is still not accurately determined, the distinction of MIH and LGIF based on size alone is questionable (Table 2). Further characterization of both of these peptides should resolve this difference.

### Old Peptides in New Places

The availability of synthetic peptides and antisera to peptides has opened up new areas in comparative endocrinology (Tables 1 and 2). Several peptides originally isolated from insects and vertebrates have been found and characterized in crustaceans. Sullivan (1979) first reported the presence and a role for the insect peptide proctolin in crustaceans. The pericardial organs contain this peptide which has a cardioexcititory action in vitro. Proctolin can also depolarize cells of the cardiac ganglion (Miller and Sullivan 1981). Proctolin was found in several sites including abdominal motor neurons (Bishop et al. 1984; Kingan and Titmus 1983). Proctolin has been colocalized with 5-HT, but haemolymph levels have not yet been reported (Kravitz et al. 1983).

An insulinlike peptide has been found in lobster, *H. americanus*, tissues (Sanders 1983a, 1983b, 1983c). The highest concentration of the peptide was in the hepatopancreas; little was found in the eyestalk. The insulinlike peptide was extracted from the hepatopancreas; the peptide stimulated glycogenesis, but had no glucostatic function (Sanders 1983a, 1983b). Sanders hypotheized that the insulinlike peptide was involved in protein metabolism, other roles being possible (Sanders 1983c).

Mancillas et al. (1981) reported that enkephalin, one of the vertebrate opioid peptides, was present in the eyestalk neuroendocrine system of the lobster *Panulirus interruptus*. The sinus gland of the lobster contained immunoreactive substance P and enkephalin, but no function was demonstrated for either peptide. Quackenbush and Fingerman (1984b) found that exogenous enkephalin induced the release of chromatophorotropins from the isolated eyestalk of the crab *Uca pugilator*. This response to enkephalin was blocked by naloxone, an opiate antagonist. This suggested that the crab possessed a natural enkephalin receptor. This is an unusual role for enkephalin, which generally inhibits cellular activity (O'Donahue and Dorsa 1982). Fingerman et al. (1985) located immunoreactive met- and leu-enkephalin in the eyestalk of the *U. pugilator*. These observations taken together support the role of enkephalin in the regulation of the chromatophorotropic system in *Uca*. Fingerman et al. (1985) also reported the presence of the peptide FMRFamide in the eyestalk of the fiddler crab, which extended the initial observation of Jacobs and VanHerp (1984) who found immunoreactive FMRFamide in a prawn. The role of FMRF in crustaceans is not known, but it does not directly affect pigment translocation in chromatophores (Greenberg et al. 1985). Crustacean RPCH is active in the traditional bioassay for FMRFamide, which further complicates this picture (Greenberg et al. 1985).

Substance P, somatostatin, neurophysin, and vasopressin have all been found in classical crustacean neuroendocrine centers (Fingerman et al. 1985; Mancillas et al. 1981; Martin and Dubois 1981; VanHerp and Bellon-Humbert 1982). Vasopressin and neurophysin were found in the Organ of Bellonci of a shrimp (VanHerp and Bellon-Humbert 1982). However, Steele (1984), after an extensive study of the Organ of Bellonci, concluded that it was a sensory structure and not a neuroendocrine structure in the amphipod. Perhaps there is a real difference between the amphipods and the decapods in this regard. Gastrinlike and cholecystokininlike peptides have been found and extracted from the gut of a crab, *Cancer magister* (Larson and Vigna 1983a, 1983b). No role is established in crustaceans, but these peptides are known to regulate gut function and act as neuromodulators.

## Terpenoid Hormones in Crustacea

Terpenoid hormones are unique to arthropods, the most common being the juvenile hormones (JH-I, JH-II, JH-III) (Downer and Laufer 1983; Raabe 1982). JH treatments of arthropods other than insects have usually been ineffective, suggesting that they did not naturally use terpenoids as hormones (Jegla 1982; Hinsch 1980). Charniaux-Cotton's description of the androgenic gland led the way to the first demonstration of terpenoid functions in crustaceans (Charniaux-Cotton 1985; Ferezou et al. 1977a, 1977b). The androgenic gland of the crab *Carcinus maenus* produces and releases a terpenoid, farnesylacetone, which inhibits ovarian development in females and stimulates protein synthesis in the testis (Berreur-Bonnenfant and Lawrence 1984; Ferezou et al. 1977b). Farnesylacetone does not stimulate spermiogenesis (Ferezou et al. 1977b). Like insect JH, farnesylacetone is synthesized through the mevalonic acid pathway (Ferezou and Barbier 1978).

Studies of the mandibular organ of Crustacea have noted its similar appearance to tissues and cells which produce steroids (Hinsch 1977, 1981; Johnson 1980; LeRoux 1968; Sochasky et al. 1972; Yudin et al. 1980). Several authors have tried to extract or measure ecdysteroids from the mandibular organ, but without success (Johnson 1980 for review; Yudin et al. 1980). Couch et al. (1978) reported that the mandibular organ of *H. americanus* contained progesterone; haemolymph levels of progesterone were found to be 40−58 pg/mL. Implants of mandibular organ can stimulate vitellogenesis and accelerate the molt cycle (Hinsch 1980; Yudin et al. 1980). Eyestalk ablation induces hypertrophy of the mandibular organ in

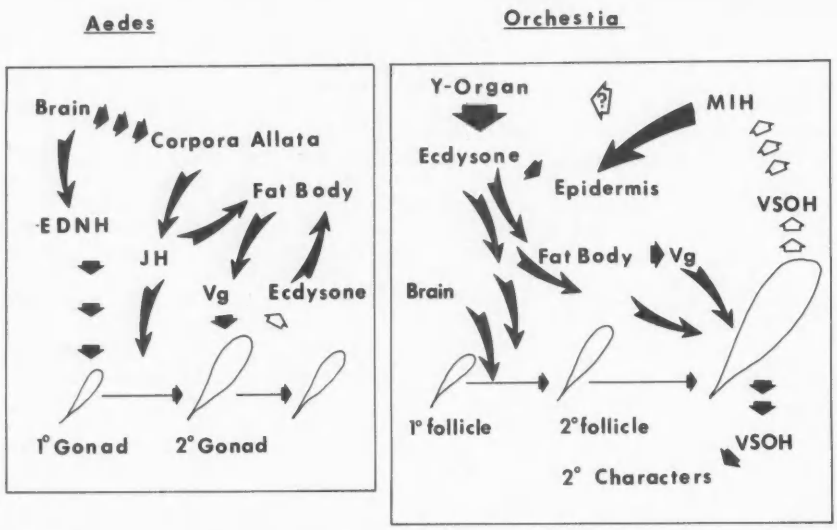


FIG. 5. Models for control of reproduction in insects (Hanaoka and Hagadorn 1980) and in amphipods (Blanchet-Tournier 1982). EDNH = egg development neurosecretory hormone, JH = juvenile hormone, Vg = vitellogenin, VSOH = vitellogenin stimulating ovarian hormone, and MIH = molt inhibiting hormone. These models do not apply to all insects or all crustaceans, but do provide frameworks for future testing.

prawns (LeRoux 1983) and in spider crabs (Hinsch 1977). Laufer et al. (1984) reported that isolated mandibular organs from the spider crab *Libinia emarginata* produce a JH-like compound. These observations have been extended to include another crab, *Callinectes sapidus*, and the lobster *H. americanus* (Laufer et al. 1984). Methylfarnesoate (MF) was identified as the primary product of the mandibular gland in vitro. The isolated glands produce 5−20 ng MF/h, which has a JH activity in insects (Laufer et al. 1985). In insects, JH is produced and released from the corpora allata, a structure that looks like a steroid-producing tissue (Wigglesworth 1970). Therefore, it may be that the primary role of the crustacean mandibular organ is closer to the insect corpora allata than was previously thought. Several laboratories are working on the role of these compounds in crustaceans, so this will be a very active area of research in the coming years.

## Biogenic Amines in Crustacea

Several recent reviews of neurotransmitter action in crustaceans are available (Atwood 1982; Cooke and Sullivan 1982; Fingerman 1985). The best known neurotransmitters in crustaceans are acetylcholine (ACh), GABA, and glutamate (Atwood 1982). Dopamine (DA), histamine (HA), norepinephrine (NE), octopamine (OA), and 5-HT have all been found in crustaceans, and their actions and roles are under intensive study (Cooke and Sullivan 1982; Fingerman 1985; Kravitz et al. 1983). Biogenic amines circulating in the haemolymph of crustaceans, invertebrates, and other animals have been reclassified as neuromodulators, extending their role beyond direct neural transmission (Barchas et al. 1978; Kupfermann 1979). The central nervous system of crustaceans contains variable quantities of biogenic amines. The pericardial organs are the best known site for biogenic amine release into the haemolymph, but other sites are possible (Claiborne and Selverston 1984; Cooke and Sullivan 1982; Elofsson et al. 1982; Fingerman 1985; Kravitz et al. 1983; Myhrberg et al. 1979).

The biogenic amines have well-studied actions on neuromuscular junction, cardiac muscle, cardiac ganglia, central pattern generators, and peptide hormones (Cooke and Sullivan 1982; Marder 1984; Miller et al. 1984) (Table 4). In homarid lobsters, 5-HT circulates in the haemolymph (1−2 n*M*). Exogenous serotonin produces a stereotyped tonic flexion of postural muscles, resulting in a "serotonin posture" (Harris-Warrick and Kravitz 1984; Kravitz et al. 1983). This posture is similar to natural postures associated with agonistic and sexual behavior (Atema and Cobb 1980). OA also circulates in lobster haemolymph (1−2 n*M*), and exogenous OA produces a tonic extension in the postural muscles. The resulting "octopamine posture" is also similar to previously described postures associated with loss of an agonistic encounter or "playing dead" (Atema and Cobb 1980; Harris-Warrick and Kravitz 1984). Exogenous OA produces a whole suite of responses: decreased time of haemolymph clotting, cardiac excitation, and hindgut contracture. OA increases cyclic AMP in cardiac muscle, abdominal muscle, and ganglia. These physiological responses could be associated with a behavioral description of escape (Cooke and Sullivan 1982 for review).

Biogenic amines release peptide neurohormones from neuroendocrine structures in several crustaceans (Fingerman 1985 for review). Biogenic amines can stimulate (5-HT, DA, and NE) and inhibit (GABA and OA) the release of chromatophorotropins in vivo and in vitro (Fingerman 1985; Quackenbush and Fingerman 1984b). 5-HT has been found to induce the release of MIH from the isolated eyestalk (Mattson and Spaziani 1985b). 5-HT can also effect a hyperglycemia in intact crayfish, which suggests that it releases CHH from the eyestalk (Keller and Beyer 1968). Peptide hormones and biogenic amines have been found to occur in the same nerve. It is

TABLE 4. Biogenic amines in crustaceans. Eye = eyestalk; TG = thoracic ganglion; Br = brain; PO = pericardial organ; SG = sinus gland. See Tables 2 and 3 for descriptions of methods and the text for compound names.

| Name | Site | Method | Action | Reference |
|---|---|---|---|---|
| 5-HT | Eye, TG, Br, PO, haemolymph | HPLC/histology | Muscle/nerve/ pigments | Fingerman 1985 |
| DA | Eye, TG, Br, PO | HPLC/histology | Muscle/nerve/ pigments | Cooke and Sullivan 1982 |
| NA | Eye, TG, Br | HPLC/histology | Muscle/nerve/ pigments | Fingerman 1985 |
| OCT | Eye, TG, Br, PO, haemolymph | HPLC/histology | Nerve/pigments | Elofsson et al. 1982 |
| HA | SG | Histology/isolated | Nerve/pigments | Claiborne and Selverston 1984 |
| GABA | TG, eye | Histology/isolated | Nerve/pigments | Fingerman 1985 |
| MIH (?) | Eye | Isolated/bioassay | Molt | Soyez and Kleinholz 1977 |

suggested that the peptide would modulate the action of the traditional neurotransmitter (Lundberg and Hokfelt 1983; Kravitz et al. 1983). These interactions of peptides and biogenic amines provide another layer of complexity to the crustacean neuroendocrine system.

The most dramatic change in comparative endocrinology in the last 5 yr is the number of pure neurohormones that are available. Immunocytochemical analysis of neuroendocrine centers in crustaceans has demonstrated several new classes of peptide neurohormones. Purification studies are continuing on several crustacean peptides, including MIH and GIH. The radioimmunoassay of ecdysteroids provides new details of the control of the molt cycle. The in vitro culture of the Y-organs will allow the exploration of cellular mechanisms of steroidogenesis. The recent characterization of terpenoid hormones in crustaceans opens an entirely new area for comparative endocrinologists. Studies of biogenic amines have shown novel relationships and roles in the regulation of peptide hormones. Research directed towards the understanding of the interrelations of these various classes of crustacean hormones is needed. Future efforts should focus on the interplay of several endocrine systems regulating crustacean physiology, as well as the details of endocrine stimulation at the cellular level.

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## References

ACHE, B. W., AND D. L. MACMILLIAN. 1980. Neurobiology, p. 165–202. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Academic Press, New York, NY.

ADIYODI, R. G., AND T. SUBRAMONIAM. 1983. Arthropoda — Crustacea, p. 443–496. *In* K. G. Adiyodi and R. G. Adiyodi [ed.] Reproductive biology of invertebrates. John Wiley & Sons, New York, NY.

AIKEN, D. E. 1980. Molting and Growth, p. 91–147. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Academic Press, New York, NY.

ARECHIGA, H., R. J. A. ATKINSON, AND J. A. WILLIAMS. 1980. Neurohormonal basis of circadian rhythmicity in *Nephrops norvegicus*. Mar. Behav. Physiol. 7: 185–197.

ARECHIGA, H., C. CABRERA-PERALTA, AND A. HUBERMAN. 1979a. Functional characterization of the neurodepressing hormone in the crayfish. J. Neurobiol. 4: 409–422.

ARECHIGA, H., J. L. CORTES, U. GARCIA, AND L. RODRIGUEZ-SOSA. 1985. Neuroendocrine correlates of circadian rhythmicity in crustaceans. Am. Zool. 25: 265–274.

ARECHIGA, H., AND A. HUBERMAN. 1980. Hormonal modulation of circadian behavior in crustaceans. Front. Hormone Res. 6: 16–34.

ARECHIGA, H., J. A. WILLIAMS, R. S. V. PULLIN, AND E. NAYLOR. 1979b. Cross-sensitivity to neuro-depressing hormone and its effect on locomotor rhythmicity in two different groups of crustaceans. Gen. Comp. Endocrinol. 37: 350–357.

ARSENAULT, A. L. 1981. The X-organ – sinus gland complex and neurohormone release during the molt cycle of the lobster, *Homarus americanus*. A light and electron microscopic study. Ph.D. thesis, Dalhousie University, Halifax, N.S.

ATEMA, J., AND J. S. COBB. 1980. Social behavior, p. 409–451. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Academic Press, New York, NY.

ATWOOD, H. L. 1982. Synapses and neurotransmitters, p. 105–150. *In* D. E. Bliss, H. L. Atwood, and D. C. Sandeman [ed.] The biology of Crustacea. Vol. 3. Academic Press, New York, NY.

BALDAIA, L., P. PORCHERON, J. COIMBRA, AND P. CASSIER. 1984. Ecdysteroids in the shrimp, *Palaemon serratus*: relations with the molt cycle. Gen. Comp. Endocrinol. 55: 437–443.

BARCHAS, J. D., H. AKIL, G. R. ELLIOT, R. B. HOLMAN, AND S. J. WATSON. 1978. Behavioral neurochemistry: neuroregulators and behavioral states. Science (Wash., DC) 200: 964–973.

BERREUR-BONNENFANT, J., AND F. LAWRENCE. 1984. Comparative effect of farnesylacetone on macromolecular synthesis in gonads of crustaceans. Gen. Comp. Endocrinol. 54: 462–468.

BIRKENBEIL, H., AND M. ECKERT. 1983. Immuno-electron-microscopic evidence of ecdysteroids in Y-organ of *Orconectes limosus* (Crustacea, Decapoda). Cell Tissue Res. 233: 233–236.

BISHOP, C. A., J. J. WINE, AND M. O'SHEA. 1984. Neuropeptide proctolin in postural motorneurons of the crayfish. J. Neurosci. 4: 2001–2009.

BLANCHET-TOURNIER, M. F. 1982. Quelques aspects des interactions hormonales entre la mue et la vitellogenèse chez le Crustacé Amphipode *Orchestia gammarella* (Pallas). Reprod. Nutr. Dev. 22: 325–344.

BLISS, D. E., AND P. HOPKINS. 1973. Bioassay and characterization of crustacean limb-growth-controlling factors, p. 104–114. *In* Neurosecretion: the final neuroendocrine pathway. VI Int. Symp. Neurosecretion. Springer-Verlag, London.

BOLLENBACHER, W. E., W. V. VEDECKIS, L. I. GILBERT, AND J. D. O'CONNOR. 1975. Ecdysone titers and prothoracic gland activity during the larval–pupal development of *Manduca sexta*. Dev. Biol. 44: 46–53.

BOMIRSKI, A., M. ARENDARCZYK, E. KAWINSKA, AND L. H. KLEINHOLZ. 1981. Partial characterization of crustacean gonad-inhibiting hormone. Int. J. Invertebr. Reprod. 3: 213–220.

BOMIRSKI, A., AND E. KLEK. 1974. Action of eyestalks on the ovary in *Rithropanopeus harrisii* and *Crangon crangon* (Crustacea: Decapoda). Mar. Biol. 24: 329–337.

BRIERS, T., AND R. HUYBRECHTS. 1984. Control of vitellogenin synthesis by ecdysteroids in *Sarcophaga bullata*. Insect Biochem. 14: 121–126.

BROWN, F. A. JR., AND G. M. JONES. 1948. Ovarian inhibition by a sinus-gland principle in the fiddler crab. Biol. Bull. 96: 228–232.

BRUCE, M., AND E. S. CHANG. 1984. Demonstration of a molt-inhibiting hormone from the sinus gland of the lobster, *Homarus americanus*. Comp. Biochem. Physiol. 79A: 421–424.

CHANG, E. 1978. Identification, quantification, and metabolism of crustacean molting hormones. Ph.D. thesis, University of California, Los Angeles, CA.

1984. Ecdysteroids in Crustacea: role in reproduction, molting, and larval development, p. 223–230. *In* W. Engels, W. H. Clark, A. Fischer, P. J. W. Olive, and D. F. Went [ed.] Advances in invertebrate reproduction. Vol. 3. Elsevier, Amsterdam, The Netherlands.

1985. Hormonal control of molting in decapod Crustacea. Am. Zool. 25: 179–185.

CHANG, E., AND M. BRUCE. 1980. Ecdysteroid titers of juvenile lobsters following molt induction. J. Exp. Zool. 214: 157–160.

1981. Ecdysteroid titers of larval lobsters. Comp. Biochem. Physiol. 70A: 239–241.

CHANG, E., B. A. SAGE, AND J. D. O'CONNOR. 1976. The qualitative and quantitative determinations of ecdysones in tissues of the crab, *Pachygrapsus crassipes*, following molt induction. Gen. Comp. Endocrinol. 30: 21–33.

CHARMANTIER, G. 1980. Contrôle endocrine et neuroendocrine de la mue de puberté chez les mâles de *Sphaeroma serratum* (Fabricius, 1787) (Crustacea, Isopoda, Flabellifera). Gen. Comp. Endocrinol. 41: 349–363.

CHARNIAUX-COTTON, H. 1985. Vitellogenesis and its control in malacostracan Crustacea. Am. Zool. 25: 197–206.

CLAIBORNE, B., AND A. I. SELVERSTON. 1984. Histamine as a neurotransmitter in the stomatogastric nervous system of the spiny lobster. J. Neurosci. 4: 708–721.

COOKE, I. M., AND R. E. SULLIVAN. 1982. Hormones and neurosecretion, p. 205–290. *In* D. E. Bliss, H. L. Atwood, and D. C. Sandeman [ed.] The biology of Crustacea. Vol. 3. Academic Press, New York, NY.

COUCH, E., C. A. ADEJUWON, S. J. SEGAL, AND S. S. KOIDE. 1978. Ultrastructural study and radioimmunological evidence for progesterone production on the mandibular gland of the lobster, *Homarus americanus*. Biol. Bull. 157: 364. (Abstr.)

DEHN, P. F., D. E. AIKEN, AND S. L. WADDY. 1983. Aspects of vitellogenesis in the lobster, *Homarus americanus*. Can. Tech. Rep. Fish. Aquat. Sci. 1161: 24 p.

DE LOOF, A., T. BRIERS, AND R. HUYBRECHTS. 1984. Presence and function of ecdysteroids in adult insects. Comp. Biochem. Physiol. 79B: 505–509.

DOWNER, R. G. H., AND H. LAUFER. 1983. Endocrinology of insects. Liss, Inc., New York, NY.

EASTMAN-REKS, S., AND M. FINGERMAN. 1984. Effects of neuroendocrine tissue and cyclic-AMP on ovarian growth in vivo and in vitro in the fiddler crab, *Uca pugilator*. Comp. Biochem. Physiol. 79A: 679–684.

ELOFSSON, R., L. LAXMYR, E. ROSENGREN, AND C. HANSSON. 1982. Indentification and quantitative measurements of biogenic amines and DOPA in the central nervous system and haemolymph of the crayfish, *Pasifastacus leniusculus*. Comp. Biochem. Physiol. 71C: 195–201.

FEREZOU, J. P., AND M. BARBIER. 1978. Biosynthèse de la farnésylacétone-(E,E) par les glandes androgènes du crabe, *Carcinus maenas*. Helv. Chim. Acta 61: 669–674.

FEREZOU, J. P., J. BERREUR-BONNENFANT, J. J. MEUSY, M. BARBIER, SUCHY, AND H. K. WIPF. 1977a. 6,10,14-Trimethylpentadecan-2-one and 6,10,14-trimethyl-5-trans,9-trans,13-pentadecatrien-2-one from the androgenic glands of the male crab, *Carcinus maenas*. Experientia 33: 290.

FEREZOU, J. P., J. BERREUR-BONNENFANT, A. TEKITEK, M. ROJAS, M. BARBIER, M. SUCHY, H. K. WIPF, AND J. J. MEUSY. 1977b. Biologically-active lipids from the androgenic gland of the crab, *Carcinus maenas*, p. 361–366. *In* D. J. Faulkner and W. H. Fenical [ed.] Marine natural products chemistry. Plenum Press, New York, NY.

FERNLUND, P., AND L. JOSEFSSON. 1972. Crustacean color change hormone: amino acid sequence and chemical synthesis. Science (Wash., DC) 177: 173–175.

FINGERMAN, M. 1963. The control of chromatophores. MacMillian, New York, NY.

1985. The physiology and pharmacology of crustacean chromatophores. Am. Zool. 25: 233–252.

FINGERMAN, M., M. M. HANUMANTE, G. K. KULKARNI, R. IKEDA, AND L. VACCA. 1985. Localization of substance-P-like, leucine-enkephalin-like, methionine-enkephalin-like and FMRFamide-like immunoreactivity in the eyestalk of the fiddler crab, *Uca pugilator*. Cell Tissue Res. 241: 473–477.

FREEMAN, J. A. 1980. Hormonal control of chitinolytic activity in the integument of *Balanus amphitrite*, *in vitro*. Comp. Biochem. Physiol. 65A: 13–17.

FREEMAN, J. A., AND J. D. COSTLOW. 1979. Hormonal control of apolysis in barnacle mantle tissue epidermis, *in vitro*. J. Exp. Zool. 210: 333–346.

FYHN, U. E. H., H. J. FYHN, AND J. D. COSTLOW. 1977. Cirripede vitellogenesis: effect of ecdysterone *in vitro*. Gen. Comp. Endocrinol. 32: 266–271.

GOHAR, M., AND C. SOUTY. 1984. Action temporelle d'ecdysteroides sur la synthèse protéique ovarienne in vitro chez le Crustacé isopode terrestre *Porcellio dilatatus*. Reprod. Nutr. Dév. 24: 137–145.

GORGELS-KALLEN, J. L., AND F. VANHERP. 1981. Localization of crustacean hyperglycemic hormone (CHH) in the X-organ sinus gland complex in the eyestalk of the crayfish, *Astacus leptodactylus* (Nordmann, 1842). J. Morphol. 170: 347–355.

GREENBERG, M. J., AND D. A. PRICE. 1983. Invertebrate neuropeptides: native and naturalized. Annu. Rev. Physiol. 45: 271–288.

GREENBERG, M. J., K. R. RAO, H. K. LEHMAN, D. A. PRICE, AND K. E. DOBLE. 1985. Cross-phyletic bioactivity of arthropod neurohormones and molluscan ganglion extracts: evidence of an extended peptide family. J. Exp. Zool. 233: 337–346.

HANAOKA, K., AND H. H. HAGADORN. 1980. Brain hormone control of ecdysone secretion by the ovary in a mosquito, p. 467–480. *In* J. A. Hoffman [ed.] Progress in ecdysone research. Elsevier, Amsterdam, The Netherlands.

HARRIS-WARRICK, R. M., AND E. A. KRAVITZ. 1984. Cellular mechanisms for modulation of posture by octopamine and serotonin in the lobster. J. Neurosci. 4: 1976–1993.

HERREID, C. F., AND S. M. MOONEY. 1984. Color change in exercising crabs: evidence for a hormone. J. Comp. Physiol. 154: 207–212.

HINSCH, G. W. 1977. Fine structural changes in the mandibular gland of the male spider crab, *Libinia emarginata* (L.) following eyestalk ablation. J. Morphol. 154: 307–316.

1980. Effect of mandibular organ implants upon the spider crab ovary. Trans. Am. Microsc. Soc. 99: 317–322.

1981. The mandibular organ of the female spider crab, *Libinia emarginata*, in immature, mature and ovigerous crabs. J. Morphol. 168: 181–187.

HINSCH, G. W., AND D. C. BENNETT. 1979. Vitellogenesis stimulated by thoracic ganglion implants into destalked immature spider crabs, *Libinia emarginata*. Tissue Cell 11: 345–351.

HOKFELT, T., O. JOHANSSON, A. LJUNGDAHL, J. M. LUNDBERG, AND M. SCHULTZBERG. 1980. Peptidergic neurons. Nature (Lond). 284: 515–524.

HOPKINS, P. M. 1982. Growth and regeneration patterns in the fiddler crabs, *Uca pugilator*. Biol. Bull. 163: 301–319.

1983. Patterns of serum ecdysteroids during induced and uninduced proecdysis in the fiddler crab, *Uca pugilator*. Gen. Comp. Endocrinol. 52: 350–356.

1986. Ecdysteroid titers and Y-organ activity during late intermolt and proecdysis in the fiddler crab, *Uca pugilator*. Gen. Comp. Endocrinol. 63: 362–373.

HOPKINS, P. M., D. E. BLISS, S. W. SHEEHAN, AND J. R. BOYER. 1979. Limb growth-controlling factors in the crab, *Gecarcinus lateralis*, with special reference to limb growth-inhibiting factor. Gen. Comp. Endocrinol. 39: 192–207.

HUBERMAN, A., H. ARECHIGA, A. CIMET, J. ROSA, AND C. ARAMBURO. 1979. Isolation and purification of a neurodepressing hormone from the eyestalk of *Procambarus bouvieri* (Ortmann) Eur. J. Biochem. 99: 203–208.

JACOBS, A. A. C., AND F. VANHERP. 1984. Immunocytochemical localization of a substance in the eyestalk of the prawn, *Palaemon serratus*, reactive with an anti-FMRF-amide rabbit serum. Cell Tissue Res. 235: 601–605.

JAFFE, H., M. LOEB, D. K. HAYES, N. TALBOT, AND S. GARVICK. 1984. Isolation of crustacean erythrophore concentrating hormone from nerve tissue of *Homarus americanus*. Comp. Biochem. Physiol. 78C: 397–401.

JAROS, P. P., AND R. KELLER. 1979. Immunocytochemical identification of hyperglycemic hormone-producing cells in the eyestalk of *Carcinus maenas*. Cell Tissue Res. 204: 379–385.

JEGLA, T. C. 1982. A review of the molting physiology of the trilobite larva of *Limulus*, p. 83–101. *In* J. Bonaventura, C. Bonaventura, and S. Tesh [ed.] Physiology and biology of horseshoe crabs: studies on normal and environmentally stressed animals. Liss, Inc., New York, NY.

JEGLA, T. C., AND J. D. COSTLOW. 1979. The *Limulus* bioassay for ecdysteroids. Biol. Bull. 156: 103–114.

JOHNSON, P. T. 1980. Histology of the blue crab, *Callinectes sapidus*: a model for the decapoda. Praeger, New York, NY.

JOSEFSSON, L. 1983a. Invertebrate neuropeptide hormones. Int. J. Pept. Protein Res. 21: 459–470.

1983b. Chemical properties and physiological actions of crustacean chromatophorotropins. Am. Zool. 23: 507–515.

KELLER, R. 1983. Biochemistry and specificity of neurohemal hormones in Crustacea, p. 118–148. *In* A. P. Gupta [ed.] Neurohemal organs of arthropods. Thomas Co., Springfield, IL.

KELLER, R., AND E. M. ANDREW. 1973. The site of action of the crustacean hyperglycemic hormone. Gen. Comp. Endocrinol. 20: 572–3578.

KELLER, R., AND J. BEYER. 1968. Zur hyperglykamischen Wirkung von Sero-

tonin und Augestielextrakt beim Flusskrebs, *Orconectes limosus*. Z. Vgl. Physiol. 59: 78–85.

KELLER, R., P. P. JAROS, AND G. KEGEL. 1985. Crustacean hyperglycemic neuropeptides. Am. Zool. 25: 207–221.

KELLER, R., AND G. KEGEL. 1984. Studies on crustacean eyestalk neuropeptides by use of high performance liquid chromatography, p. 145–154. *In* J. Hoffman and M. Porchet [ed.] Biosynthesis, metabolism, and mode of action of invertebrate hormones. Springer-Verlag, Berlin.

KINGAN, T., AND M. TITMUS. 1983. Radioimmunologic detection of proctolin in arthropods. Comp. Biochem. Physiol. 74C: 75–78.

KLEINHOLZ, L. H., AND R. KELLER. 1979. Endocrine regulation in Crustacea, p. 159–214. *In* E. J. W. Barrington [ed.] Hormones and evolution. Academic Press, New York, NY.

KOOLMAN, J., AND K. D. SPINDLER. 1983. Mechanism of action of ecdysteroids, p. 179–201. *In* R. G. H. Downer and H. Laufer [ed.] Endocrinology of insects. Liss, Inc., New York, NY.

KRAVITZ, E. A., B. S. BELTZ, S. GLUSMAN, M. F. GOY, R. M. HARRIS-WARRICK, M. F. JOHNSTON, M. S. LIVINGSTONE, T. L. SCHWARTZ, AND K. K. SIWICKI. 1983. Neurohormones and lobsters: biochemistry to behavior. Trends Neurosci. 6: 346–349.

KUPFERMANN, I. 1979. Modulatory actions of neurotransmitters. Annu. Rev. Neurosci. 2: 447–465.

LACHAISE, F., AND J. A. HOFFMANN. 1977. Ecdysone et développement ovarien chez un Décapode, *Carcinus maenas*. C.R. Acad. Sci. Paris 285D: 701–704.

LARSON, B. A., AND S. R. VIGNA. 1983a. Species and tissue distribution of cholecystokinin/gastrin-like substances in some invertebrates. Gen. Comp. Endocrinol. 50: 469–475.

1983b. Gastrin/cholecystokinin-like immunoreactive peptides in the Dungeness crab, *Cancer magister* (Dana): immunochemical and biological characterization. Regul. Pept. 7: 155–170.

LAUFER, H., D. W. BORST, C. CARRASCO, F. C. BAKER, AND D. A. SCHOOLEY. 1984. The detection of juvenile hormone in Crustacea. Am. Zool 24: 33A. (Abstr.)

1985. Juvenile hormone-like compounds in Crustacea. X Int. Symp. Comp. Endocrinol., Colorado. (Abstr.)

LEROUX, A. 1968. Description d'organes mandibulaires nouveaux chez les Crustacés Decapodes. C.R. Acad. Sci. Paris 266D: 1414–1417.

1983. Rèactions de l'organe mandibulaires à l'ablation des pédoncules oculaires chez les larves et les juvéniles de *Palaemonetes yarians* (Leach) (Decapoda, Natantia). C.R. Acad. Sci. Paris 296: 697–700.

LONDERSHAUSEN, M., AND K. D. SPINDLER. 1985. Uptake and binding of moulting hormones in crayfish. Am. Zool. 25: 187–196.

LUNDBERG, J. M., AND T. HOKFELT. 1983. Coexistence of peptides and classical neurotransmitters. Trends Neurosci. 6: 325–333.

MANCILLAS, J. R., J. F. MCGINTY, A. I. SELVERSTON, H. KARTEN, AND F. E. BLOOM. 1981. Immunocytochemical localization of enkephalin and substance P in retina and eyestalk neurones of lobster. Nature (Lond.) 293: 576–578.

MARDER, E. 1984. Mechanisms underlying neurotransmitter modulation of a neuronal circuit. Trends Neurosci. 7: 48–53.

MARTIN, G., AND M. P. DUBOIS. 1981. A somatostatin-like antigen in the nervous system of an isopod, *Porcellio dilatatus*. Gen. Comp. Endocrinol. 45: 125–130.

MARTIN, G., P. P. JAROS, G. BESSE, AND R. KELLER. 1984a. The hyperglycemic neuropeptide of the terrestial isopod, *Porcellio dilatatus*. 2. Immunocytochemical demonstration in neurosecretory structures of the nervous system. Gen. Comp. Endocrinol. 55: 217–226.

MARTIN, G., R. KELLER, G. KEGEL, G. BESSE, AND P. P. JAROS. 1984b. The hyperglycemic neuropeptide of the terrestial isopod, *Porcellio dilatatus*. 1. Isolation and characterization. Gen Comp. Endocrinol. 55: 208–216.

MATTSON, M. P., AND E. SPAZIANI. 1985a. Stress reduces hemolymph ecdysteroid levels in the crab: mediation by the eyestalks. J. Exp. Zool. 234: 319–323.

1985b. 5-Hydroxytryptamine mediates release of molt-inhibiting hormone activity from isolated crab eyestalk ganglia. Biol. Bull. 169: 246–255.

MCCONAUGHA, J. R. 1980. Identification of the Y-organ in larval stages of the crab, *Cancer anthonyi* Rathburn. J. Morphol. 164: 83–88.

MILLER, M. W., J. A. BENSON, AND A. BERLIND. 1984. Excitatory effects of dopamine on the cardiac ganglia of the crabs *Portunus sanguinolentus* and *Podophthalmus vigil*. J. Exp. Biol. 108: 97–118.

MILLER, M. W., AND R. E. SULLIVAN. 1981. Some effects of proctolin on the cardiac ganglion of the Maine lobster, *Homarus americanus*. J. Neurobiol. 12: 629–639.

MYHRBERG, H. E., R. ELOFSSON, R. ARMANT, N. KLEMM, AND L. LAXMYR. 1979. Selective uptake of exogenous catecholamines into nerve fibers in crustaceans: a fluorescence histochemical investigation. Comp. Biochem. Physiol. 62C: 141–150.

NEWCOMB, R. W. 1983. Peptides in the sinus gland of *Cardisoma carnifex:* isolation and amino acid analysis. J. Comp. Physiol. 153: 207–221.

NEWCOMB, R. W., E. STUENKEL, AND I. COOKE. 1985. Characterization, biosynthesis, and release of neuropeptides from the X-organ – sinus gland system of the crab, *Cardisoma carnifex*. Am. Zool. 25: 157–171.

O'CONNOR, J. D. 1985. Radioimmunoassay and the characterization of crustacean ecdysteroids. Am. Zool. 25: 173–178.

O'DONAHUE, T. L., AND D. M. DORSA. 1982. The opimelanotropinergic neuronal and endocrine systems. Peptides 3: 353–395.

OTSU, T., AND K. I. HANAOKA. 1951. Relation between body weight and precocious differentiation of ova in eyestalkless crabs. Bull. Yamagata Univ. (Nat. Sci.) 1: 269–274.

PANOUSE, J. B. 1943. Influence de l'ablation du péduncle oculaire sur la croissance de l'ovaire chez la Crevette *Leander serratus*. C.R. Acad. Sci. Paris 217: 553–555.

QUACKENBUSH, L. S., AND M. FINGERMAN. 1984a. Regulation of the release of chromatophorotropic neurohormones from the isolated eyestalk of the fiddler crab, *Uca pugilator*. Biol. Bull. 166: 237–250.

1984b. Regulation of neurohormone release in the fiddler crab, *Uca pugilator*: effects of gamma-aminobutyric acid, octopamine, met-enkephalin, and beta-endorphin. Comp. Biochem. Physiol. 79C: 77–84.

1984c. Purification of black pigment dispersing hormone from the fiddler crab, *Uca pugilator*. Am. Zool. 24: 95A. (Abstr.)

1985. Enzyme-linked immunosorbent assay of black pigment dispersing hormone from the fiddler crab, *Uca pugilator*. Gen. Comp. Endocrinol. 57: 438–444.

QUACKENBUSH, L. S., AND W. F. HERRNKIND. 1981. Regulation of molt and gonadal development in the spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): effect of eyestalk ablation. Comp. Biochem. Physiol. 69A: 523–527.

1983a. Regulation of the molt cycle of the spiny lobster, *Panulirus argus*: effect of photoperiod. Comp. Biochem. Physiol. 76A: 259–263.

1983b. Partial characterization of eyestalk hormones controlling molt and gonadal development in the spiny lobster, *Panulirus argus*. J. Crustacean Biol. 3: 34–44.

RAABE, M. 1982. Insect neurohormones. Plenum, New York, NY. 352 p.

RAO, K. R. 1965. Isolation and partial characterization of the molt-inhibiting hormone of the crustacean eyestalk. Experientia 21: 593–595.

1985. Pigmentary effectors, p. 395–462. *In* D. E. Bliss and L. H. Mantel [ed.] The biology of Crustacea. Vol. 9. Academic Press, New York, NY.

RAO, K. R., AND M. FINGERMAN. 1983. Regulation of release and mode of action of crustacean chromatophorotropins. Am. Zool. 23: 517–527.

RIEHM, J. P., AND K. R. RAO. 1982. Structure activity relationships of a pigment-dispersing crustacean neurohormone. Peptides 3: 643–647.

SANDERS, B. 1983a. Insulin-like peptides in the lobster, *Homarus americanus*. 1. Insulin immunoreactivity. Gen. Comp. Endocrinol. 50: 366–373.

1983b. Insulin-like peptides in the lobster, *Homarus americanus*. 2. Insulin-like biological activity. Gen. Comp. Endocrinol. 50: 374–377.

1983c. Insulin-like peptides in the lobster, *Homarus americanus*. 3. No glucostatic role. Gen. Comp. Endocrinol. 50: 378–382.

SEDLMEIER, D. 1985. Mode of action of the crustacean hyperglycemic hormone. Am. Zool. 25: 223–232.

SKINNER, D. E. 1985a. Interacting factors in the control of the crustacean molt cycle. Am. Zool. 25: 275–284.

1985b. Molting and regeneration, p. 43–145. *In* D. E. Bliss and L. H. Mantel [ed.] The biology of Crustacea. Vol. 9. Academic Press, New York, NY.

SOCHASKY, J. B., D. E. AIKEN, AND N. H. F. WATSON. 1972. Y organ, molting gland, and mandibular organ: a problem in decapod crustacea. Can. J. Zool. 50: 993–997.

SOUMOFF, C., AND J. D. O'CONNOR. 1982. Repression of Y-organ secretory activity by moltinhibiting hormone in the crab, *Pachygrapsus crassipes*. Gen Comp. Endocrinol. 48: 432–439.

SOUMOFF, C., AND D. M. SKINNER. 1980. Effect of Y-organectomy and autonomy on circulating ecdysteroid levels and regeneration in the crab, *Gecarcinus*. Am. Zool. 20: 1182. (Abstr.)

SOYEZ, D., AND L. H. KLEINHOLZ. 1977. Molt-inhibiting factor from the crustacean eyestalk. Gen. Comp. Endocrinol. 31: 233–242.

SPINDLER, K. D., R. KELLER, AND J. D. O'CONNOR. 1980. The role of ecdysteroids in the crustacean molting cycle, p. 247–280. *In* J. A. Hoffmann [ed.] Progress in ecdysone research. Elsevier, Amsterdam, The

Netherlands.

STEELE, V. J. 1984. Morphology and ultrastructure of the organ of Bellonci in the marine amphipod, *Gammarus setosus*. J. Morphol. 181: 97–131.

STEVENSON, J. R., P. W. ARMSTRONG, E. S. CHANG, AND J. D. O'CONNOR. 1979. Ecdysone titers during the molt cycle of the crayfish, *Orconectes sanborni*. Gen. Comp. Endocrinol. 39: 20–25.

STUENKEL, E. L. 1983. Biosynthesis and axonal transport of proteins and identified peptide hormones in the X-organ sinus gland neurosecretory system. J. Comp. Physiol. 153: 191–205.

SULLIVAN. R. E. 1979. A proctolin-like peptide in crab pericardial organs. J. Exp. Zool. 210: 543–552.

SULLIVAN, R. E., B. FRIEND, AND R. MCCAMAN. 1976. Endogenous levels of octopamine, serotonin, dopamine and acetylcholine in spiny lobster pericardial organs. Neurosci. Abstr. 2: 335.

TAMM, G. R., AND J. S. COBB. 1978. Behavior and the crustacean molt cycle: changes in agression of *Homarus americanus*. Science (Wash., DC) 200: 79–81.

TELFORD, M. 1968a. Changes in blood sugar composition during the molt cycle of the lobster, *Homarus americanus*. Comp. Biochem. Physiol. 26: 917–926.

1968b. The effects of stress on blood sugar composition of the lobster, *Homarus americanus*. Can. J. Zool. 46: 819–826.

VANHERP, F., AND C. BELLON-HUMBERT. 1982. Localisation immunocytochemique de substances apparentées à la neurophysine et à la vasopressine dans le pédoncule oculaire de *Palaemon serratus*, Pennant (Crustace Decapode Natantia). C.R. Acad. Sci. Paris 295: 97–102.

WHITEHEAD, D. L. 1983. Steroids, the earliest hormones. Nature (Lond.) 306: 540.

WIGGLESWORTH, V. B. 1970. Insect hormones. Freeman and Co., San Francisco, CA.

YUDIN, A. I., R. A. DIENER, W. H. CLARK JR., AND E. S. CHANG. 1980. Mandibular gland of the blue crab, *Callinectes sapidus*. Biol. Bull. 159: 760–772.

ZELENY, C. 1095. The relation of the degree of injury to the rate of regeneration. J. Exp. Zool. 2: 347–369.

ZUCKER, N. 1980, Social inhibition of courtship in neotropical fiddler crabs. Am. Zool. 20: 727. (Abstr.)

1984. Delayed courtship in the fiddler crab, *Uca musica terpsichores*. Anim. Behav. 32: 735–742.

# Review of Sexual Selection and Chemical Communication in the Lobster, *Homarus americanus*

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Field and laboratory observations have shown that female lobsters, *Homarus americanus*, are the active searching partner in courtship, choosing locally dominant males. The attractive features of the male are suspected to be intrasexual aggressive behavior and chemical cues. Size-based dominance is an important factor allowing males to secure a suitable mating shelter. In nature, male and female lobsters often approach and check shelters of other lobsters. This behavior may allow the animals to monitor the observed daily and seasonal changes in their physical and social environment. Premolt females approach the dominant male's shelter frequently in the weeks before the female's molt. Indirect evidence indicates that the female then "blows" a urine-related sex pheromone into the male shelter. One to several days before molting, a female enters the male shelter. Female intrasexual competition increases the premolt, but not the postmolt, cohabitation period. During cohabitation, males fan with their pleopods blowing a strong current through the shelter and into the environment. This chemical advertisement attracts other females, including future mating partners, to his shelter entrance. Females spent 1–2 wk in the male shelter. Mating takes place 30 min after the female molts. Another female may start cohabitation with the male immediately. In one 10-wk period a dominant male in the laboratory cohabited and mated with five females in sequence; females ignored a second male of equal size. Theoretically, by allowing a female to spend time in his shelter the male foregoes other mating opportunities, but this is balanced — and hence a stable strategy — by his protection of a vulnerable postmolt female who carries his offspring. Females must choose males who can protect them efficiently from predation and, perhaps more importantly, from competing lobsters.

Des observations effectuées sur le terrain et en laboratoire montrent que la femelle du homard *Homarus americanus* joue le rôle actif dans la recherche du partenaire en choisissant un mâle dominant. Les caractéristiques attirantes du mâle semblent être un comportement agressif intrasexuel et des signaux chimiques. La dominance par la taille constitue un facteur important qui permet aux mâles de trouver un abri convenant à l'accouplement. Dans le milieu naturel, les homards mâles et femelles vont souvent s'approcher des abris d'autres homards pour les examiner. Ce comportement leur permet peut-être de surveiller les modifications quotidiennes et saisonnières de leur milieu physique et social. Les femelles en période de prémue s'approchent souvent de l'abri du mâle dominant dans les semaines qui précèdent la mue. Certaines indications montrent indirectement que la femelle émet alors dans l'abri du mâle une phéromone sexuelle liée à l'urine. Un ou plusieurs jours avant la mue, une femelle pénètre dans l'abri du mâle. La concurrence intrasexuelle des femelles fait augmenter la période de cohabitation avant, mais non après la mue. Pendant la cohabitation, les mâles agitent leurs pléopodes, créant ainsi un fort courant qui traverse l'abri et en sort. Ce signal chimique attire d'autres femelles, parmi lesquelles se trouvent de futures partenaires, vers l'entrée de l'abri. Les femelles passent 1 à 2 sem dans l'abri. L'accouplement a lieu 30 min après la mue de la femelle. Un autre femelle peut commencer immédiatement à cohabiter avec le mâle. Au cours d'une période de 10 sem, un mâle dominant du laboratoire a cohabité et s'est accouplé avec cinq femelles à la suite; les femelles ont ignoré un autre mâle de taille égale. En théorie, en permettant à une femelle de passer du temps dans son abri, le mâle annule d'autres possibilités d'accouplement, mais ce phénomène est compensé (ce qui constitue une stratégie de stabilité) par le fait qu'il protège ainsi une femelle vulnérable en post-mue qui porte sa progéniture. Les femelles doivent choisir des mâles qui peuvent les protéger efficacement de la prédation et, aspect peut-être plus important, des autres homards.

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In this paper I review the evidence for sexual selection, competition, and chemical communication in the lobster, *Homarus americanus*. This updates information in reviews by Atema and Cobb (1980), Salmon (1983), and Dunham (1986). The first observations of courtship behavior in this species were reported recently (Atema et al. 1979). Prior to this, Templeman (1934, 1936) showed that *H. americanus* mates best when the female has just molted and up to a week or so thereafter. There were also reports of intermolt matings (review in Dunham 1978). In the absence of information on courtship, mate selection, and social behavior in general, intermolt matings were speculated to be useful to animals that were believed to be nonsocial and to live widely dispersed on the sea bottom. Intermolt mating, it was reasoned, would allow the female to collect sperm at any time she happened to cross paths with a mature male.

Female sex pheromones had been suspected to exist since Hughes and Matthiessen (1962) mentioned the attractiveness of tank water of freshly molted females, which was subsequently described in more detail (McLeese 1970, 1973; Atema and

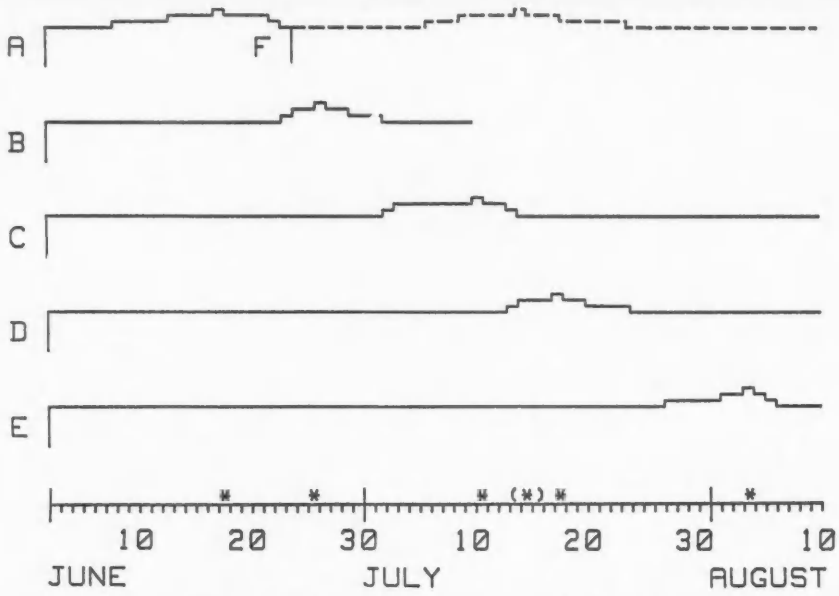


FIG. 1. Staggering of female molts and cohabitations. Over a 10-wk period, five females (A–E) cohabited with the dominant of two males, staggering their molts. In each line the first step up is intermittent premolt shelter sharing, the second is permanent premolt shelter sharing, the third is the day of female molt and mating, and the next two down are permanent and intermittent postmolt shelter sharing. In one case, females C and D were observed alternating in the male shelter: C postmolt, D premolt. Female F was introduced replacing A. She first courted the dominant male who cohabited with B, C, and D in sequence. F then cohabited with the subordinate male. Asterisks indicate female molt dates.

Engstrom 1971). Perhaps these discoveries should have prompted investigations into lobster courtship, because sex pheromones typically are courtship signals. Unfortunately, it was assumed that (as in many insect species) the female was the sedentary dispenser of a chemical lure that would attract males. Attempts to isolate a female pheromone have failed (McLeese et al. 1977; J. Atema, unpubl.), probably due to lack of proper understanding of natural courtship behavior. Social stimuli presented to males in isolation frequently led to habituation and stimulus generalization (J. Atema, unpubl.).

A series of laboratory (Atema et al. 1979; J. Atema, E. B. Karnofsky, and R. H. Elgin, unpubl.) and field (Karnofsky and Atema 1979; E. B. Karnofsky, J. Atema, and R. H. Elgin, unpubl.) observations of lobster behavior were initiated which lasted from 1973 to 1981. A different picture emerged of lobster social behavior and particularly of courtship. The latter will be summarized below before reviewing our more recent studies on sexual selection and chemical communication (Atema and Cowan 1986; Cowan and Atema 1985).

## Courtship Sequence

Using snorkle and small flashlights in a shallow lobster habitat, it was possible to observe behavior of undisturbed lobsters at night over a 3-yr period. Marked individuals could be followed for up to 13 mo. The interpretation of field events was facilitated by simultaneous long-term observations of eight lobsters, four males and four females, in each of two large naturalistic aquaria (Atema et al. 1979; J. Atema et al., unpubl.).

These studies showed that during the weeks before molting, mature females approach the shelters of preferred males with increasing frequency. One at a time they stand at the entrance facing it and after some seconds leave again. Sometimes the male comes to the entrance, usually after the female has left. Eventually one of the females enters; in the field she molts the following morning, and laboratory observations show that a brief, one-time mating follows the end of molting by about 30 min. Both laboratory and field observations show that the female stays with the male in his shelter for about a week. During a cohabitation, several other females may approach the shelter entrance, probably attracted by a male-generated odor plume. A next female may enter the male shelter the same night that the first one leaves; after about a week she too leaves.

In the field the preferred male was once seen to "run" to the shelter of another male and evict him. In the laboratory, such evictions by the preferred male were common. Since the preferred male was always dominant in agonistic encounters in the laboratory, we assume that in the field the preferred male is locally dominant. In one series of field observations the dominant male molted and left his shelter after a sequence of two 1-wk pair bonds, probably because molt-related loss of dominance caused him to be evicted by another male. After the originally dominant male left, females were no longer seen checking the entrance of that shelter or even the area. In the laboratory, one dominant male mated in sequence with five females; all but one female waited her turn rather than mate with the other similar-sized male in the tank (Fig. 1). In the field, where lobsters come and go, daily shelter checking may be required to keep track of important mating partners and competitors. Such checking is an important feature of laboratory behavior as well: the most dominant animals are checked

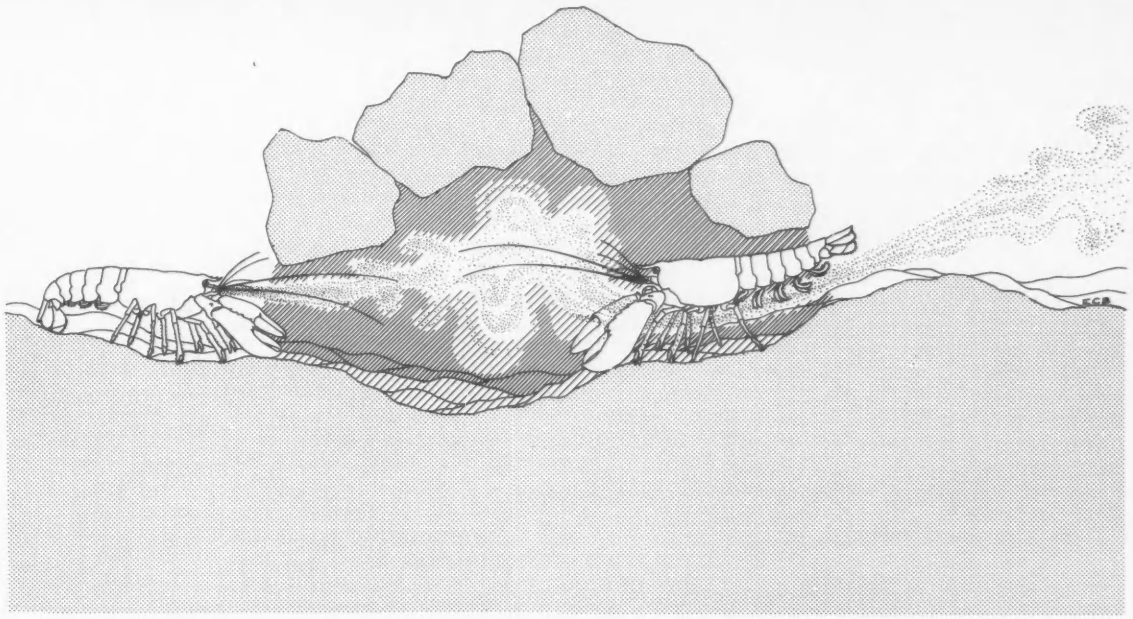

FIG. 2. Female courting male with pheromone plume (artist's concept). The female on the left injects her gill current into the male's shelter; he responds by retreating to the opposite entrance and fanning his pleopods. Water flows from female to male and into the environment.

most frequently (Cowan and Atema 1985). In laboratory studies, we confirmed that mature premolt females frequently approach the shelter of the dominant male, spend a few days of intermittent shelter sharing, and finally one to several days of permanent shelter sharing before molting and mating (Atema et al. 1979). This is followed by a postcopulatory guarding period of about 5 d, ending with one to several days of intermittent shelter sharing. Various interesting and puzzling behaviors were seen in connection with courtship, such as boxing, fanning, and knighting (see Atema and Cobb (1980) for a description of behavior units). The possible functions of these behaviors have become better understood recently.

The field and naturalistic laboratory studies have provided evidence for (1) female mate choice, (2) intrasexual competition, (3) pre- and post-copulatory guarding, (4) serial polygamy, (5) male and female dominance, (6) courtship signals and odor plumes, and (7) male advertising. In addition there is suggestive evidence for (8) behavioral/pheromonal regulation of the molt cycle and (9) a male molt strategy. These will now be discussed.

## 1. Female Mate Choice

All observations show that females, not males, make the initial mate choice (Atema et al. 1979; E. B. Karnofsky et al., unpubl.; Cowan and Atema 1985). Males establish a stable residence and appear to dominate other males in the area (and often females as well) by evictions. They wait in their shelter for premolt females to visit. The shelter entrances of the most dominant animal are checked most frequently by the other animals in the tanks. There is a direct correlation between dominance order and the frequency of being checked (Cowan and Atema 1985). At present there is no evidence that males reject courting females. There is some evidence that intermolt females are rejected, perhaps because at that time they lack the proper sex pheromone (Atema and Engstrom 1971). The male attributes upon which females base their choice need to be investigated. There is evidence for male "advertising" during cohabitation (section 7), but it is not known what attracts the first female of the season nor which male signals correspond to desirable genotype.

## 2. Intrasexual Competition

Considering that females make the initial mate choice, it is not surprising to find clear evidence for intrasexual competition in males. Field evidence (E. B. Karnofsky et al., unpubl.) shows that a mating male evicted a nearby male of similar size by making a straight line approach and then returned home; he himself was not evicted until he molted. Larger animals also prevailed in shelter evictions, although smaller males could defend their shelters against larger females. Laboratory evidence (Atema et al. 1979) shows that the largest of four males present was dominant in agonistic encounters and became the only mating male; he regularly evicted others, male and female, from their shelters. These were mostly temporary evictions. In another laboratory study (J. Atema and D. Cowan, unpubl.) with two males of identical size, the male who was preferred by all females was clearly dominant and also regularly evicted others from shelters, particularly the other male. In one instance, he evicted the other male, who was then in a period of postcopulatory guarding, by running right through his shelter while ignoring the female entirely. This instance underscores the potential importance for females to select the dominant male as a mating partner.

Presently, evidence for female competition is weak. When five females of similar size were placed in a large naturalistic tank with two males (Fig. 1), all five mated in sequence with the dominant male (Cowan and Atema 1985). When a molted female was replaced with a new premolt female, the latter

immediately began to approach the shelter of the dominant male. She continued to do so frequently for several days, but since he was cohabiting in sequence with two females already there, she became the only one cohabiting and mating with the other male; as described above, his ability to protect a postmolt female was poor. The fact that five females staggered their molt dates and mated in sequence would imply strong female competition for access to the dominant male. Hence, we expected that if a female dominance order exists, it would correlate with their molt order: the most dominant female molting first, etc.

The five females maintained a rather stable dominance order among themselves, which was broken only when an individual female molted and returned from cohabitation still partially soft-shelled with resultant loss of dominance. However, this dominance order did not correspond to their molt order. The female dominance order corresponded to occupation of preferred shelters. We do not understand at present why shelter entrances of dominant females are checked more frequently than those of other females. Perhaps other females check to see if the better shelters have become vacated.

### 3. Pre- and Post-copulatory Guarding: Pair Bond

Laboratory studies (Atema et al. 1979; Cowan and Atema 1985) showed detailed evidence for pair bonding (i.e. male and female cohabiting for reproductive/parental purposes and excluding other mating partners). Field studies (E. B. Karnofsky et al., unpubl.) confirmed these observations with pieces of direct and indirect evidence: about 1 wk of permanent shelter sharing occurs during which time the male rarely leaves and the female does not leave at all. Irregular shelter sharing takes place with the same female: one to several days preceding and one to several days following permanent shelter sharing. While other females, particularly premolt females, show interest in the mating shelter (section 7) by frequent approaches and living in shelters nearby, they do not enter; and if occasionally they try, they are repelled by the male (or the female if she is still premolt). During cohabitation the male on occasion leaves the shelter to pursue and chase an animal that had tried to enter. The only observation of a cohabiting male who could not defend his shelter against another male was described in section 2. In the field his female might have found a dominant male in a nearby area; equally likely, the subdominant male would not have remained so close to the dominant male. In the tank the animals had no other choice: they could not leave the tank and apparently the female could not postpone molting at the molt stage in which she was introduced into the tank.

The pair bonding process is a period of courtship, during which the female at first approaches the preferred male's shelter entrance without entering and blows her gill current into his shelter; this current may be spiked with urine injections (section 6) and may contain her sex pheromone(s). He responds by retreating to the other shelter entrance, raising his tail, and, with his pleopods, fanning water (with the female odor) through the shelter (Fig. 2). When she tries to enter they box, claws to claws. Generally, after repeated approaches which may extend over several days, she enters and the male retreats deep into his shelter. Details of these behaviors are described in section 6. During the premolt period of intermittent shelter sharing the entrance rituals are repeated whenever the male or the female enters the shelter. Boxing is rare during the postmolt period. Fanning by the male continues throughout cohabitation.

The biological function of the 1-wk pair bond may be primarily to assure the female protection during her most vulnerable postmolt days. In addition, it provides the male with a compromise between two alternatives: mating with more females (if each cohabitation period were shorter or absent) and protecting his mate, the key to his biological success, for even longer periods of time. The 1-wk "compromise" may be sufficient for the female to harden her new shell and still allow the male access to other females. The lobster's pair bond is an example of pre- and post-copulatory guarding. Since females are likely to mate with other males in the week after they molt, postcopulatory guarding may serve not only to prevent predation on the female but also her access to other males. A recent discovery shows that older females who molt (and mate) only every other or every third year can fertilize each yearly batch of eggs from one insemination (Waddy and Aiken 1986). This would be a very strong enforcer of postcopulatory guarding, because the male would insure his contribution to not only one but several year classes of progeny by mating with one such female. This discovery also removes the last doubts that may exist about the necessity for intermolt matings: these are not necessary because sperm can be stored and used for several years.

In terms of sexual selection theory, the male benefits most from postcopulatory guarding by preventing his female access to other males. And it benefits the female because predation on the postmolt female would affect the female's lifetime reproductive success more than the male's. However, the precopulatory cohabitation period may benefit the female more than the male: it allows her to temporarily monopolize the dominant male. We would expect, then, when female competition is great that dominant females have longer cohabitations, particularly premolt. There is now evidence that increased female competition results in increased duration of premolt cohabitation regardless of female dominance (J. Atema and D. Cowan, unpubl.).

### 4. Serial Polygyny

Based on Wilson's (1975, p. 327) definition, lobsters are not monogamous (i.e. for at least a breeding season "one male and one female join to rear at least a single brood"), but practice serial polygamy, which "implies the formation of at least a temporary pair bond." The most common form of polygamy is polygyny: one male pairing with several females. This is the case in *H. americanus*. The one case of evidence for serial polygyny in the field has been described above: a male spending 1 wk each with two females, one female following the other within hours. In the laboratory, strong evidence comes from the experiment where five females staggered their molting and mated in sequence with the same male (Fig. 1). Each spent approximately 1 wk with that male, and in some cases two females traded places within the same day. The rather precise staggering of female molting is far from expected when considering the molt peaks seen in the field: there, molting of mostly immature females is highly concentrated in the first 2 wk of June.

An intriguing question is what controls the female molt cycle. Theory would predict that the male would help control the observed female molt staggering, since it is to his advantage to space out the available females at 1- to 2-wk intervals. Thus far there is no evidence for either male or female control over female molt cycles. Yet, the discovery of molt-specific male

and female substances (section 6) may point to the possibility of pheromonal control over reproductive biology (section 8).

## 5. Male and Female Dominance

Both short-term staged fights (Scrivener 1971) and long-term naturalistic aquarium observations (J. Atema et al., unpubl.) show that dominance in lobsters is almost entirely size dependent; there is good evidence that males are dominant over females, even when the female is somewhat larger (review in Atema and Cobb 1980). The precise interaction between size and sex has not been established. The only field evidence of size and sex influences on dominance comes from an analysis of observed shelter evictions: generally, larger animals successfully evicted smaller ones, except in a number of cases where larger females could not evict smaller males (E. B. Karnofsky et al., unpubl.).

It appears that in lobsters, dominance functions to gain preferential access to shelters. One must assume that shelters serve males and females equally in protection against predation. However, mature males must in addition secure shelters suitable for cohabitation if they are to attract females and become reproductively successful. Thus, dominance may be more important for them than for females. If so, one might expect males at least within a certain size range to be dominant over females. The evidence supports this at present. Intrasexual competition would tend to favor somewhat separate male and female dominance orders: female dominance for preferential access to the dominant male, and male dominance to establish a mating shelter. Male dominance was directly correlated with mating success (Atema et al. 1979; J. Atema and D. Cowan, unpubl.). Female dominance was not correlated with first access to the preferred male (Cowan and Atema 1985); perhaps it functions to allow a dominant female to take up shelter near the dominant male. A size-based dominance order in which males dominate nearly equal-sized females would accommodate the separate male and female reproductive interests. It appears to fit the presently scattered and incomplete data.

If male dominance is indeed so important to their reproductive success, then one would expect them to develop means to secure dominance. In laboratory studies a small difference in claw size (Scrivener 1971; Atema and Cobb 1980) is highly predictive for the outcome of a staged fight. Such fights often involve claw wrestling. With such evidence, one would expect male emphasis on large claws. Indeed, at the size of first maturity, as estimated by successful mating of females (Atema et al. 1979), and by physiological gonadal maturity (Templeman 1935; Aiken and Waddy 1986), the sexes begin to diverge noticeably in relative body proportions: males grow larger claws, females broader abdomens (Templeman 1935; Lang et al. 1977). The male investment in large claws starting at maturity may be primarily an adaptation to establish dominance in the region. In addition — one could speculate — large claws could serve as a mate selection signal for females, but it remains to be shown that females can ascertain claw size during courtship. Female abdomen broadening increases the size of her brood pouch in which the eggs develop for some 8–11 mo until they hatch. The fitness value of this adaptation is obvious: it increases the number of eggs that can be carried. Here again, it is not known if a broad tail conveys other advantages such as in female attractiveness or mating success.

## 6. Courtship Signals and Odor Plumes

A number of behaviors appear connected with courtship and the subsequent week of shelter sharing. However, most of these behaviors are not exclusive to these phases in the animal's life cycle; they just occur more frequently, or in different context than otherwise. The descriptions are based on 12 yr of observations of lobsters in naturalistic aquaria (Atema et al. 1979; J. Atema and D. Cowan, unpubl.). Field evidence is not available, because these behaviors take place inside the male shelter which precludes observation under almost all circumstances.

"Boxing" is a somewhat ritualized exchange of jabs with closed claws. The jabs vary in intensity from slow and gentle to fast and powerful equalling those seen in aggressive exchanges outside a mating context. Boxing occurs as part of the entrance "ceremony" when the female enters the male shelter whether for the first time or during the period of intermittent shelter sharing. Both animals may box, or one may simply keep its claws as a shield in front. During early courtship the male boxes a female shield; during cohabitation it is often reversed. Boxing bouts may last seconds to minutes and the frequency varies from a poke once in a while to one every second for about 10 s. Boxing also occurs during cohabitation when the female moves around inside the shelter causing the male to box. Either male or female may initiate boxing and the other may or may not respond. In the hour(s) before the female molts, her boxing often increases; some females can be quite violent. During this period the male generally retreats to one of the entrances where he fans his pleopods (see below); he no longer boxes.

"Knighting" is a term used to describe the posture of the female that is often (and exclusively) seen during the hour before she begins molting. It consists of the female placing her claw(s) on top of the male facing her. Knighting can last from one to several seconds and involve one or both claws. It can happen in the middle of boxing. In response, the male usually freezes his posture. We now interpret this behavior in connection with chemical communication: with the gill current the female may blow her chemical signal directly in his "face." Knowing the mechanics of this gill current, there is, indeed, no possibility that this is *not* happening! But why she needs to get so close is not clear, since she has been producing this gill current all along and the shelter must be permeated with her odor. One might suspect that during knighting, females either produce a stronger signal or a different signal, perhaps injected with the urine, to indicate her impending molt. During her molting the male stands by very quietly and after her molting he approaches her occasionally. He appears "quietly attentive." Mating follows molting by 30 min almost exactly every time (see also Atema et al. 1979, table 2). Thus, it is possible that the female signal during knighting serves at once as a timing signal for mating, and to ensure her of the male's presence and nonaggression during her most vulnerable period: the molting process itself and immediately afterwards.

"High-on-legs" is a mostly male behavior. It was described also as "mating dance" (Atema and Engstrom 1971) and resembles male crab mating postures (Gleeson 1980): the animal stands with legs stretched raised high off the bottom. It is seen during cohabitation. It was the only male-specific behavior that was significantly correlated with the presentation of female molt body odor and intermolt urine (Atema and Cowan 1986).

"Fanning" causes water currents resulting in odor plumes (Atema 1985). It takes place regularly, but is especially apparent during courtship. Lobsters generate three different currents and use two different fan behaviors: "pleopod fan" and "exopodite fan." Pleopod beating (with tail raised) results in a

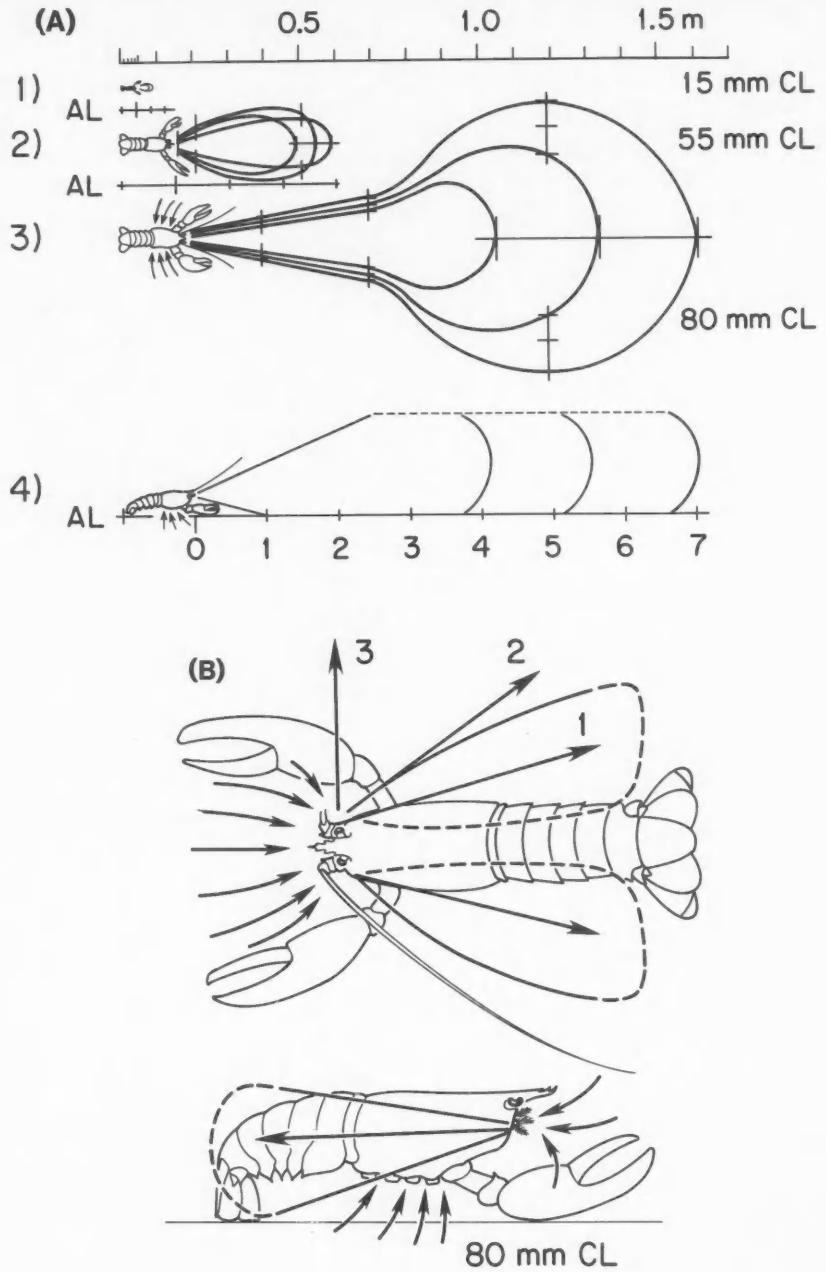


FIG. 3. Gill and exopodite currents (from dye visualizations). (A) The gill current enters (arrows) between the walking legs and exits through a small anterior pore under the antennae. 1, extent of gill current in postlarval (15 mm CL) lobster; 2, extent of gill current in juvenile (55 mm CL) lobster; 3 and 4, top and side view of mature (80 mm CL) lobster. AL = animal length; abscissa measured in units of total body length of the particular animal from rostrum to telson; CL = carapace length; common size indication of lobsters, measured from rear of eye socket to posterior margin of carapace. A scale in metres is given at the top of the figure. From Atema (1985). (B) Top and side view of exopodite current of mature lobster. 1, Most common direction; 2 and 3, expodite currents that have been seen occasionally. The exopodite current deflects the continuous gill current and also draws water from an anterior hemisphere of about 5 cm radius.

strong current drawn from front to rear underneath the animal. Exopodite fan (caused by the concerted beating of the fanlike exopodites of the three maxillipeds) reverses the gill current which normally extends many animal lengths in front of every breathing lobster (Fig. 3) (McPhie and Atema 1984; Atema 1985). The gill current is caused by the peristaltic pumping action of the scaphognatite. Urine released from the nephropores situated directly above the exit pores of the gill chambers is automatically injected into this strong continuous gill current. This current is critical for respiration — without scaphognatites, lobsters die within hours — and is not under voluntary control. Exopodite fanning is voluntary and allows the animal to reverse the gill current so that chemical cues are not projected forward; instead, water from anterior regions is drawn toward the animal and its chemistry can be sampled with the antennules or other anterior chemoreceptors. From the visible occurrence of exopodite fanning we can infer the currents around the lobster: when exopodite fanning, the gill current is reversed, otherwise it projects forward.

An example of the use of fan currents is seen when a courting female approaches a male shelter: she often does not fan, so that she projects her gill current toward the male. In response, the male fans both his pleopods and exopodites, thus reversing his gill current and directing two currents from anterior to posterior: the odor flow is entirely from female to male (Fig. 2). A second example of fanning is the male "advertizing" to be described next.

7. Male Advertizing

In the context of lobster courtship where females locate a preferred male in his shelter, it is to be expected that males with suitable shelters "advertise" their presence to females, analogous to male birds singing from their territories. In nocturnal animals, such as lobsters, the mode of advertisement might well be chemical. Recent evidence shows strong female responses to male intermolt urine (Atema and Cowan 1986). In order to broadcast his odor the male must send it off in a current, either the forward gill current or the rearward pleopod current.

At present there is no information on how the male attracts his first female of the season. However, pleopod fanning is a very obvious behavior associated — among many other uses — with cohabiting males; there is a direct correlation between the intensity and frequency of male pleopod fanning and the stage of cohabitation: he fans least when not cohabiting, more during intermittent sharing of his shelter, more yet during permanent sharing, and most on the day of molting (Cowan and Atema 1985). During fanning bouts he stands typically inside the shelter with his tail stretched toward one of the entrances (Fig. 2): pleopod fanning will then cause a strong current to be drawn through the shelter. Fanning may have several functions, and all need to be tested experimentally. It may help him obtain the odor of another lobster (as in Fig. 2), it may help him obtain general chemical information about the environment outside his shelter, it may advertize his shelter to females and male rivals, and during cohabitation it may advertize his mating status to other females. Indeed, mating shelters are the center of attraction for all lobsters in naturalistic tanks. Similarly, in the field they are frequently visited (E. B. Karnofsky et al., unpubl.).

8. Behavioral (Pheromonal) Regulation of the Molt Cycle

From the rather precise staggering of the molt dates of five females in a naturalistic aquarium (Fig. 1), one might infer that some kind of exogenous control is exerted over the (endocrine-regulated) molt cycle of mature females. This is particularly obvious from a comparison with (mostly immature) female molting observed in the field, where a typical clustering is seen in the beginning of the molting season, the first weeks of June. While the mechanisms for such exogeneous control remain obscure, it is not unreasonable to suspect chemical signals either from the male or between the females. Since no correlation between female dominance order and molt order was found, one might suspect some form of male control. Indeed, his very obvious pleopod fanning may have such a function. Pheromonal control over female reproductive endocrinology is common in social rodents and eusocial insects.

Mature male molting also seems to be under some external regulation which may depend on the mating status (see section 9). While the selective advantages are intuitively obvious, the mechanisms remain unknown.

9. Male Molt Strategy

During a string of successive cohabitations the male should not molt. Dominant males in captivity can lose their dominant position for a month or more after molting (J. Atema et al., unpubl.). The preferred male who mated with five females in succession from June through September did not molt until December (J. Atema and D. Cowan, unpubl.). The male observed in the field, who mated with two females in sequence and then molted, lost his shelter, and was not seen afterward (E. B. Karnofsky et al., unpubl.). Male reproductive success will be improved by a simple strategy: a male who is successful in establishing an attractive mating shelter should postpone molting until the available females have all molted; a male who is not successful in establishing a mating shelter should give up and molt as soon as possible to increase size and outcompete currently successful males. It is not known to what degree this strategy is used but the unsuccessful male (who was ignored by five females in sequence in favor of an equal-sized male rival) molted in early August while his rival continued cohabiting (J. Atema and D. Cowan, unpubl.).

## Life History Strategy and Conclusion

Courtship is only one aspect of an animal's biology; it must fit into its life history together with many other physiological, behavioral, and environmental requirements, all of which interact directly or indirectly. To attempt a concluding statement on lobster courtship, I want to place it in the context of its life history, starting with the requirement to place offspring in an advantageous environment. The American lobster allows its larvae to develop to an advanced larval stage inside the egg and under maternal care. The larvae are released in June when the water temperature begins to approach its yearly high and larval food is abundant. This allows the larvae to grow rapidly. To avoid losing the brood or the new sperm, mature female molting must be timed after larval release and before mating; by tying mating to molting the female gains the maximum possible yearly interval in which to carry eggs and still molt. After reaching a certain size she begins to molt less frequently, thus making it possible to produce a new clutch of eggs as soon as the previous one has hatched. This necessitates either sperm storage and multiple-year fertilization from one mating, or additional yearly intermolt matings. There is compelling evi-

dence for the former (Waddy and Aiken 1986). A broader tail allows females to raise larger brood sizes. Female size is directly proportional to reproductive success. Thus, males should compete for larger females, particularly those large enough to have multiple broods from one fertilization. To become fertilized the female selects a dominant male who can protect her from competing females and predation during her soft-shelled postmolt state. In competition with other females she benefits from a long cohabitation period in which she can monopolize the dominant male. This necessitates behavioral/pheromonal control over the female molt cycle when several females are competing. As in most polygamous mating systems, lobsters have female mate selection: female investment in eggs and brood care is greater than the male's.

The male perspective interacts with this female scenario. Mature males must establish a mating shelter and advertize their presence, dominance, and, when possible, proven mating success to females. They do this by fanning their odor into the environment and particularly the odor of their shelter during cohabitation. Since a good shelter is essential to their mating success, they must be dominant over males as well as females because both sexes need shelters. Their enlarged claws may be adaptations to accomplish this. To dominate the most desirable large females the male must be larger or at least of comparable size. Indeed, males grow faster than females. This may have additional physiological reasons: females put energy into egg production, males into body growth. To mate with as many females as possible, males may control female molt cycles in situations of severe female competition for one male. The male should attempt to keep the cohabitation as short as possible but not so short that the female would still find another male to mate with or be too vulnerable to predation. The length of cohabitation may thus be a compromise between male and female interests. Considering that cohabiting females mate only once very briefly 30 min after molting, it is surprising — given our current, still incomplete knowledge of lobster behavior — that they are behaviorally and physiologically receptive for several (up to 12) days after molting. Yet, Templeman (1934) observed that females begin to show courtship resistence after 12 h.

Sexual selection in lobsters appears to correspond well to the general theories developed in behavioral ecology (Krebs and Davies 1978). A number of behaviors point to chemical signals as important means of inter- and intra-specific communication.

## Acknowledgements

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## References

AIKEN, D. W., AND S. L. WADDY. 1986. Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective. Can. J. Fish. Aquat. Sci. 43: 2258–2270.

ATEMA, J. 1985. Chemoreception in the sea: adaptations of chemoreceptors and behavior to aquatic stimulus conditions. Soc. Exp. Biol. Symp. 39: 387–423.

ATEMA, J., AND J. S. COBB. 1980. Social behavior, p. 409–450. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

ATEMA, J., AND D. COWAN. 1986. Behavioral responses of lobsters (*Homarus americanus*) to conspecific odors: sex-identifying molt and urine signals. J. Chem. Ecol. 12: 2065–2080.

ATEMA, J., AND D. G. ENGSTROM. 1971. Sex pheromone in the lobster, *Homarus americanus*. Nature (Lond.) 232: 261–263.

ATEMA, J., S. JACOBSON, E. KARNOFSKY, S. OLESZKO-SZUTS, AND L. S. STEIN. 1979. Pair formation in the lobster, *Homarus americanus*: behavioral development, pheromones and mating. Mar. Behav. Physiol. 6: 277–296.

COWAN, D., AND J. ATEMA. 1985. Serial monogamy, mate choice, and pre- and post-copulatory guarding in lobsters. Biol. Bull. 169: 550.

DUNHAM, P. J. 1978. Sex pheromones in Crustacea. Biol. Rev. Cambridge Philos. Soc. 53: 555–583.

1986. Pheromones and behavior in Crustacea. H. Laufer and R. Downer [ed.] *In* Invertebrate endocrinology. Vol. 2. Alan R. Liss, Inc., New York, NY. (In press)

GLEESON, R. A. 1980. Pheromone communication in the reproductive behavior of the blue crab, *Callinectes sapidus*. Mar. Behav. Physiol. 7: 119–134.

HUGHES, J. T., AND G. C. MATTHIESSEN. 1962. Observations on the biology of the American lobster, *Homarus americanus*. Limnol. Oceanogr. 7(3): 414–421.

KARNOFSKY, E. B., AND J. ATEMA. 1979. Field and laboratory observations of lobster mating behavior. Biol. Bull. 157: 374.

KREBS, J. R., AND N. B. DAVIES. 1978. Behavioural ecology. Blackwell Scientific Publications, Oxford. 494 p.

LANG, F., C. K. GOVIND, W. J. COSTELLO, AND S. I. GREENE. 1977. Developmental neuroethology: changes in escape and defense behavior during growth of the lobster. Science (Wash., DC) 197: 682–685.

MCLEESE, D. W. 1970. Detection of dissolved substances by the American lobster (*Homarus americanus*) and olfactory attraction between lobsters. J. Fish. Res. Board Can. 27: 1371–1378.

1973. Chemical communication among lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 30: 775–778.

MCLEESE, D. W., R. L. SPRAGGINS, A. K. BOSE, AND B. N. PRIMANIK. 1977. Chemical and behavioral studies of sex attractant of the lobster (*Homarus americanus*). Mar. Behav. Physiol. 4: 219–232.

MCPHIE, D., AND J. ATEMA. 1984. Chemical communication in lobsters: information currents. Biol. Bull. 167: 510–511.

SALMON, M. 1983. Courtship, mating systems and sexual selection in decapods, p. 145–169. *In* S. Rebach and D. Dunham [ed.] Studies in adaptation: the behavior of higher Crustacea. John Wiley & Sons, New York, NY.

SCRIVENER, J. C. E. 1971. Agonistic behavior of the American lobster, *Homarus americanus* (Milne-Edwards). Fish. Res. Board Can. Tech. Rep. 235: 1–128.

TEMPLEMAN, W. 1934. Mating in the American lobster. Contrib. Can. Biol. Fish. (N.S.) 8: 423–458.

1935. Local differences in the body proportions of the lobster, *Homarus americanus*. J. Biol. Board Can. 1: 213–226.

1936. Further contributions to mating in the American lobster. J. Biol. Board Can. 2: 223–226.

WADDY, S. L., AND D. E. AIKEN. 1986. Multiple fertilization and consecutive spawning in large American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2291–2294.

WILSON, E. O. 1975. Sociobiology. Belknap Press, Cambridge, MA. 697 p.

# Multiple Fertilization and Consecutive Spawning in Large American Lobsters, *Homarus americanus*

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Large female American lobsters, *Homarus americanus* (>120 mm carapace length), maintained at nearshore Bay of Fundy temperatures often spawn twice without an intervening molt (consecutive spawning). Consecutive spawning occurs in two forms: *successive-year* (spawning in two successive summers, a molt in the first and fourth years) and *alternate-year* (spawning in alternate summers, a molt in the first and fifth years). In both types, females often are able to fertilize the two successive broods with the sperm from a single insemination (multiple fertilization). Twenty of 21 large females that were held for up to 13 yr displayed one of these types of consecutive spawning. Consecutive spawning and multiple fertilization enable large lobsters to spawn more frequently over the long term than their smaller counterparts. This, combined with the logarithmic relationship between body size and numbers of eggs produced, means that very large lobsters have a much greater relative fecundity than previously thought.

Les grosses femelles de homard américain (*Homarus americanus*) (>120 mm de longueur de carapace), maintenues à la température qui règne près des côtes de la baie de Fundy, pondent souvent deux fois sans avoir de mue entre-temps (pontes consécutives). Ces pontes consécutives prennent deux formes : *deux années de suite* (pontes au cours de deux étés successifs, mue la première et la quatrième année), et *une année sur deux* (ponte la deuxième et la quatrième année, mue la première et la cinquième année). Dans les deux cas, les femelles sont souvent capables de féconder les deux portées successives avec le sperme provenant d'une seule insémination (fécondation multiple). Vingt des 21 grosses femelles observées pendant une période allant jusqu'à 13 ans ont montré l'un de ces types de pontes consécutives. Ces pontes et la fécondation multiple permettent aux gros homards de pondre plus fréquemment à long terme que les homards de plus petite taille. Ce phénomène, combiné à la relation logarithmique entre la taille du corps et le nombre d'oeufs produits, signifie que les homards de très grande taille présentent une fécondité relative beaucoup plus forte qu'on ne le croyait jusque-là.

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The relationship between body length and fecundity is logarithmic in American lobsters, *Homarus americanus*, so one spawning from a very large female can yield more eggs than can be produced by the spawning of 10 females of minimum legal size (Aiken and Waddy 1980). Females larger than 120 mm carapace length (CL) are relatively rare in most inshore areas (Skud 1969; Thomas 1973), but in offshore and deepwater areas, large female lobsters are numerous and may represent more than 50% of the total number of legal-sized lobsters present (Campbell and Duggan 1980; Skud and Perkins 1969). Their relative fecundity in these areas is therefore much greater, especially since the proportion that is ovigerous is also exceptionally high (Skud and Perkins 1969).

However, total egg production by an individual is a function of spawning frequency as well as number of eggs produced. Mating is assumed to occur primarily when the female molts, and since females over 120 mm CL molt less frequently than females at the minimum legal size for the fishery, it was assumed that their total egg production would be reduced (see Krouse 1973). It has also been suggested that larvae from very large females would be less viable than those from smaller females (Saila and Flowers 1965).

At one time or another all of these assumptions — infrequent molting, mating, and spawning, as well as reduced larval viability — have been offered as evidence that very large females are relatively unproductive members of the lobster population and not worth protecting (Saila and Flowers 1965; see also Anonymous 1978; Thomas 1973).

In recent years the exploitation of large lobsters has increased in the offshore areas as well as in the Bay of Fundy and the southern Gulf of St. Lawrence (Campbell and Duggan 1980; Elner 1980; Pezzack and Duggan 1983). Once the residual stocks of large lobsters are gone it will be difficult to rebuild them, so it is imperative that the assumptions regarding relative egg contribution of the different size classes of lobsters be correct. This paper contains evidence that the relative fecundity of large females has been seriously underestimated.

## Methods

Twenty one female lobsters 75–195 mm CL, captured by otter trawl or commercial lobster trap in the southern Gulf of St. Lawrence, Bay of Fundy, and southwest Nova Scotia, were held individually up to 13 yr in broodstock tanks used for

TABLE 1. Molt (M) and spawning (S) cycles of female American lobsters held in the laboratory from 3 to 13 yr. Bold italics indicate a maternal size of 120 mm CL or larger.

| Source | Initial CL (mm) | Years in captivity | Years 1 | 3 | 5 | 7 | 9 | 11 | 13 |
|---|---|---|---|---|---|---|---|---|---|
| Southwest Nova Scotia | 75 | 13 | S M | S M | S M | S M | S M | S ***S*** | ***S M*** |
| Gulf of St. Lawrence | 98 | 10 | S M | S M | S M | ***S S*** | ***M S*** | | |
| Gulf of St. Lawrence | 95 | 9 | S M | S M | S M | ***S S*** | ***M*** | | |
| Bay of Fundy | 96 | 7 | M S | M S | M ***S*** | ***S*** | | | |
| Southwest Nova Scotia | 100 | 7 | M S | M S | M ***S*** | ***S*** | | | |
| Bay of Fundy | 101 | 11 | M S | M S | M ***S*** | ***M S*** | ***M S*** | ***M*** | |
| Bay of Fundy | 121 | 8 | ***S S*** | ***M S*** | ***M S*** | ***S M*** | | | |
| Bay of Fundy | 124 | 10 | ***S S*** | ***M S*** | ***M S*** | ***S M S*** | ***M*** | | |
| Bay of Fundy | 131 | 5 | ***M S*** | ***S M S*** | | | | | |
| Bay of Fundy | 133 | 3 | ***S S M*** | | | | | | |
| Bay of Fundy | 128 | 3 | ***M S S*** | | | | | | |
| Bay of Fundy | 120 | 3 | ***S S M*** | | | | | | |
| Bay of Fundy | 122 | 4 | ***S S M S*** | | | | | | |
| Bay of Fundy | 120 | 4 | ***S M S S*** | | | | | | |
| Bay of Fundy | 165 | 6 | ***M S*** — ***S M S*** | | | | | | |
| Bay of Fundy | 152 | 6 | ***M S*** — ***S M S*** | | | | | | |
| Bay of Fundy | 143 | 6 | ***M S*** — ***S M S*** | | | | | | |
| Bay of Fundy | 138 | 5 | ***M S*** — ***S M*** | | | | | | |
| Bay of Fundy | 195 | 4 | ***S*** — ***S M*** | | | | | | |
| Bay of Fundy | 146 | 5 | ***S M S*** — ***S*** | | | | | | |
| Bay of Fundy | 173 | 4 | ***S*** — ***S M*** | | | | | | |

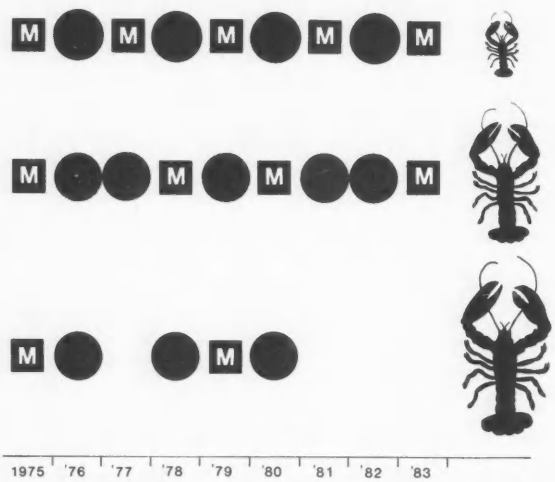


FIG. 1. Molt and spawning cycles of female American lobsters. Molt is indicated by squares and spawning by circles. Upper row: molt and spawning cycle characteristic of female lobsters <120 mm CL ($N$ = 22, with an additional 68 maintained for 6 yr); middle row: successive-year spawning cycles of lobsters >120 mm CL ($N$ = 13); lower row: alternate-year spawning cycles of lobsters >120 mm CL ($N$ = 7).

spawning and egg incubation in a lobster culture facility (Aiken and Waddy 1985). The glass-fronted tanks allowed daily checks for molting and spawning to be done without handling the lobsters. Newly molted females were placed with males and allowed to mate naturally, but otherwise the sexes were held separately.

Lobsters were fed 2–6 times per week (depending on water temperature) on a rotating diet of fresh frozen shrimp, fish, squid, euphausids, and beef liver. Temperature of the local seawater ranged from 0 to 14°C annually. Natural daylength was available through windows that faced east and west, but photoperiod was uncontrolled and subject to occasional light breaks during the dark period.

From each of 17 recently captured ovigerous lobsters (105–175 mm CL) from the Bay of Fundy, 1000–3000 larvae were fed frozen adult *Artemia* and reared to fourth stage in standard 40-L planktonkreisels (Van Olst et al. 1980) at constant 20°C.

## Results

Consecutive spawning (two egg extrusions without an intervening molt) was recorded from all but 1 of the 21 lobsters during the 13 yr of observations. All female lobsters with intermolt times of 3 yr or longer spawned twice between molts. Five of the lobsters were maintined for sufficient time to demonstrate the shift from the "typical" biennial molting and spawning pattern to one in which spawning becomes more frequent as molts become further apart. The change from the typical biennial spawning pattern to consecutive spawning occurred in all five when they molted to approximately 120 mm CL (118, 120, 121, 122, and 123 mm CL). Of the 21 females greater than 120 mm CL, only one (currently 167 mm CL) has maintained the typical biennial molting and spawning pattern.

Two types of consecutive spawning cycle were observed in these large females: *successive-year*, in which spawning occurred in successive summers (molt at 3-yr intervals), and *alternate-year*, in which females spawned the year following molt and again 2 yr later without an intervening molt (molt at 4-yr intervals). A cycle of successive-year spawning usually alternates with a cycle of typical biennial spawning (Fig. 1), but the data on alternate-year spawning are too limited to project (Table 1).

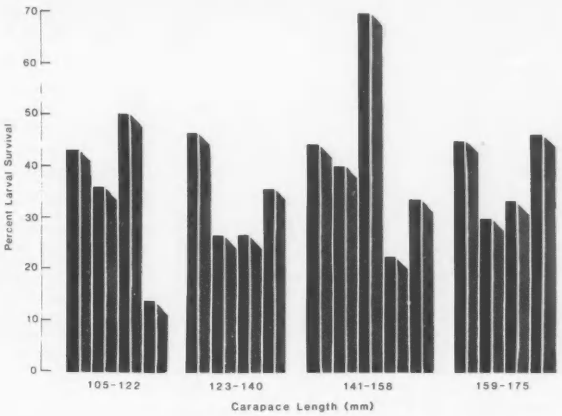


FIG. 2. Survival of larvae from first to fourth stage. Each vertical bar indicates larvae from one female lobster from the Bay of Fundy (105–175 mm CL).

Of the 22 consecutive spawnings recorded from 20 lobsters, 17 (77%) of the second broods were fertilized with sperm from a single insemination at the previous molt, 2–3 yr earlier. Four of the second broods were infertile, and one female was artificially inseminated (see Aiken et al. 1984), resulting in a fertile second brood.

Survival of larvae from first to fourth stage was determined for 17 females 105–175 mm CL. Larval survival ranged from 23 to 70% and bore no statistically significant relationship to maternal size ($r = 0.14$) (Fig. 2).

## Discussion

Although there can be exceptions in areas with cold summer water temperature (Ennis 1971; Squires et al. 1971), biennial spawning with a molt in the alternate years is the rule for inshore lobsters up to approximately 120 mm CL (Aiken and Waddy 1980). The results reported here show that although molt frequency declines with increasing size, there is no comparable decline in either spawning frequency or larval viability that can be attributed to increasing maternal size up to at least 195 mm CL.

The females we have held for many years began changing from a 2-yr to a 3-yr intermolt period at approximately 120 mm CL. This is considerably below the size estimated by egg-per-recruit models developed for the Bay of Fundy (Campbell 1985, 1986). Consecutive spawning also begins in our females at approximately 120 mm CL, perhaps reflecting a changing relationship between the dominant molting cycle and the subordinate reproductive cycle.

In any 3-yr period the small mature female on a typical biennial cycle will spawn either once (molt–spawn–molt) or twice (spawn–molt–spawn). In the same period an alternate-year spawner will spawn once (molt–spawn–nothing) and a consecutive-year spawner will spawn twice (molt–spawn–spawn). Thus, over an extended period of time, consecutive spawners will produce as many or more broods than the typical biennial spawner that molts in alternate years (Fig. 1).

An important question should be asked at this point: is consecutive spawning something that occurs in the wild, or is it an anomaly produced by confinement? Three lines of evidence suggest that consecutive spawning is a natural phenomenon: (a) the information in Table 1 shows that wild females larger than 120 mm when captured were already in the consecutive spawning mode when brought to the holding facility, whereas smaller ones already in the facility switched to the consecutive spawning mode at approximately that same size; (b) an additional 90 females, some initially as small as 63.5 mm CL, were held in these same facilities, and all matured, adopted the typical biennial cycle, and maintained it for 6 yr; (c) long-term tagging studies have recently shown that consecutive spawning does occur in the wild (Campbell 1983; D. S. Pezzack, pers. comm.).

From the recapture of 12 tagged ovigerous lobsters, Campbell (1983) estimated that only 20% of Bay of Fundy females larger than 120 mm CL are in the consecutive spawning mode. Our observations suggest that this estimate is low. It is extremely difficult to obtain the long-term data required to identify consecutive spawning in individual females in the wild. For example, if a consecutive spawner were tagged while carrying the second of two successive broods, her status as a consecutive spawner could not be conclusively established unless she were recaptured after the spawning period in each of the next 5 yr. Field data of this type are almost impossible to obtain from suitable numbers of lobsters.

In the traditional view, mating occurs when the female molts. Spermatozoa are transferred to the seminal receptacle of the female and stored until she spawns. This suggests that mating and therefore fertilization are dependent on molting and that once a female has spawned and fertilized her eggs, she must molt again to obtain spermtozoa for the next spawning. By this reasoning, large females would be able to spawn fertile eggs only as often as they molt, perhaps once in 3 or 4 yr.

Two recently recognized phenomena refute this: *multiple fertilization*, in which lobsters successfully fertilize two consecutive spawnings with the spermatozoa from a single mating, and *intermolt mating*, in which uninseminated preovigerous hardshell females mate prior to spawning (Dunham and Skinner-Jacobs 1978; Aiken and Waddy 1980). The female lobster thus has two mechanisms that remove spawning and fertilization from any dependence on molting.

The significance of the results reported here is best expressed in terms of relative fecundity — the contribution that a size class of lobster makes to the total reproductive output of a population. The absolute fecundity of large lobsters is impressive, but if they are few in number, spawn infrequently, or produce infertile eggs or weak larvae, their relative fecundity may be insignificant. As noted above, this has been the prevailing opinion.

Multiple fertilization, intermolt mating, consecutive spawning, and normal larval viability in large lobsters change this. Large lobsters are capable of spawning and fertilizing broods more frequently than smaller ones, and their eggs and larvae appear to be just as viable. Their relative fecundity is therefore a function of the absolute fecundity of individual females and the number of large females in the total population.

Absolute fecundity changes logarithmically with body size, so one very large female has the potential to produce an order of magnitude more eggs than a female half her size. The number of large females in the population is more difficult to determine, but large females are concentrated in certain areas, and they undertake seasonally directed movements. Their relative contribution to certain downstream areas may therefore be greater (and possibly more important) than their contribution to

the population as a whole. Such a mechanism has been implied for the Grand Manan fishery (Campbell and Duggan 1980), and there are other areas where comparable situations exist (Dadswell 1979). Campbell and Pezzack (1986), for example, estimated that up to 77% of eggs produced in the Bay of Fundy, southwest Nova Scotia, and the offshore areas of Georges Bank and Browns Bank are from females that come from the offshore areas where large females are common.

In view of the new information on the spawning frequency of large lobsters, the concentrations of large lobsters in certain offshore and inshore areas, and the recent intensification of fishing effort directed at these large size classes, it would seem prudent to reassess the contribution that these large lobsters make to specific stocks and to the lobster population in general.

## References


AIKEN, D. E., AND S. L. WADDY. 1980. Reproductive biology, p. 215–276. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

1985. Production of seed stock for lobster culture. Aquaculture 44: 103–114.

AIKEN, D. E., S. L. WADDY, K. MORELAND, AND S. M. POLAR. 1984. Electrically induced ejaculation and artificial insemination of the American lobster *Homarus americanus*. J. Crustacean Biol. 4: 519–527.

ANONYMOUS. 1978. American Lobster Fishery Management Plan, prepared by Lobster Sub Board. NE Marine Fisheries Board. 178 p.

CAMPBELL, A. 1983. Growth of tagged American lobsters, *Homarus americanus*, in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 40: 1667–1675.

1985. Application of a yield and egg-per-recruit model to the lobster fishery in the Bay of Fundy. N. Am. J. Fish. Manage. 5: 91–104.

1986. Implications of size and sex regulations for the lobster fishery of the Bay of Fundy and southwestern Nova Scotia, p. 126–132. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

CAMPBELL, A., AND D. R. DUGGAN. 1980. Review of the Grand Manan lobster fishery with an analysis of recent catch and effort trends. Can. Tech. Rep. Fish. Aquat. Sci. 997: 20 p.

CAMPBELL, A., AND D. S. PEZZACK. 1986. Relative egg production and abundance of berried lobsters, *Homarus americanus*, in the Bay of Fundy and off southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 43: 2190–2196.

DADSWELL, M. J. 1979. A review of the decline in lobster (*Homarus americanus*) landing in Chedabucto Bay between 1956 and 1977 with a hypothesis for a possible effect by the Canso causeway on the recruitment mechanism of eastern Nova Scotia stocks. Can. Fish. Mar. Serv. Tech. Rep. 834: 113–144.

DUNHAM. P. J., AND D. SKINNER-JACOBS. 1978. Intermolt mating in the lobster (*Homarus americanus*). Mar. Behav. Physiol. 5: 209–214.

ELNER, R. W. 1980. Lobster gear selectivity — a Canadian overview. Can. Tech. Rep. Fish. Aquat. Sci. 932: 77–84.

ENNIS, G. P. 1971. Lobster (*Homarus americanus*) fishery and biology in Bonavista Bay, Newfoundland 1966–70. Fish. Res. Board Can. Tech. Rep. 289: 46 p.

KROUSE, J. S. 1973. Maturity, sex ratio, and size composition of the natural population of american lobster, *Homarus americanus*, along the Maine coast. U.S. Dep. Commer. Fish. Bull. 71: 165–173.

PEZZACK, D. S., AND D. R. DUGGAN. 1983. The Canadian offshore lobster (*Homarus americanus*) fishery — 1971 to 1982. Int. Counc. Explor. Sea C.M. 1983/K:34.

SAILA, S. B., AND J. M. FLOWERS. 1965. A simulation study of sex ratios and regulation effects with the American lobster, *Homarus americanus*. Gulf Carribb. Fish. Inst. Univ. Miami Proc. 18: 66–78.

SKUD, B. E. 1969. The effect of fishing on size composition and sex ratio of offshore lobster stocks. Fiskeridir. Skr. Ser. Havunders. 15: 295–309.

SKUD, B. E., AND H. C. PERKINS. 1969. Size composition, sex ratio, and size maturity of offshore northern lobsters. U.S. Fish Wildlife Ser. SSR-Fish. No. 598: 10 p.

SQUIRES, H. J., G. E. TUCKER, AND G. P. ENNIS. 1971. Lobster (*Homarus americanus*) in Bay of Islands, Newfoundland, 1963–65. Fish. Res. Board Can. Tech. Rep. 1151: 58 p.

THOMAS, J. C. 1973. An analysis of the commercial lobster (*Homarus americanus*) fishery along the coast of Maine, August 1966 through December 1970. U.S. Dep. Commer. NOAA Tech. Rep. NMFS SSRF-667: 57 p.

VAN OLST, J. C., J. M. CARLBERG, AND J. T. HUGHES. 1980. Aquaculture, p. 333–384. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

# Epizootic Infestations by Nemertean Brood Parasites on Commercially Important Crustaceans

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Wickham, D. E. 1986. Epizootic infestations by nemertean brood parasites on commercially important crustaceans. Can. J. Fish. Aquat. Sci. 43: 2295–2302.

Historical literature presenting quantitative information on the interaction between nemertean brood parasites of crustaceans and their hosts is reviewed and compared with recent detailed studies on epizootics of these parasites. Observations over the last century demonstrate that nemertean infestations on most host species are of low intensity and result in relatively low levels of host brood mortality. Epizootics discovered in the last decade on certain host species have resulted in extensive egg loss in many important commercial crustacean stocks. The data at hand suggest that epizootics are primarily restricted to commercially exploited species of decapods. One implication of this is that human exploitation affects natural host–parasite balance.

L'auteur revoit les documents publiés présentant des données quantitatives sur l'interaction entre les némertiens parasites de la ponte des crustacés et leurs hôtes, et les compare à des études détaillées et récentes portant sur des épizooties de ces parasites. Les observations recueillies depuis un siècle montrent que l'infestation par les némertiens de la plupart des espèces hôtes sont de faible intensité et produisent une mortalité relativement faible de la ponte de l'hôte. Les épizooties observées au cours de la dernière décennie chez certaines espèces hôtes ont détruit de grandes quantités d'oeufs dans de nombreux stocks de crustacés exploités commercialement. Les données étudiées semblent montrer que les épizooties se produisent principalement chez les espèces exploitées de décapodes. Ce phénomène indique entre autres que l'exploitation humaine affecte l'équilibre naturel entre l'hôte et le parasite.

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Nemertean worms have been observed as symbiotes of decapod crustaceans for over a century (Kolliker 1845). The outline of their life history was recognized by the time Humes (1942) published his monograph on the genus *Carcinonemertes*. These worms begin life as planktonic larvae. The larvae settle on crab hosts and remain on the exoskeleton as juvenile worms. Worms that infest ovigerous hosts move into the host egg mass where they feed on host eggs, grow, and reproduce sexually. Worms lay their own eggs in the host brood, and worm larvae hatch near the time the host eggs hatch.

Recently, epizootic infestations by the nemertean crab egg predator *Carcinonemertes errans* have been observed on the central California population of the Dungeness crab *Cancer magister* (Wickham 1979a). Individual Dungeness crabs with as many as 100 000 worms in their egg clutches have been found. Heavily infested crabs lost all of their eggs and the overall population of crabs in most years lost over 50% of their eggs.

Up until the observations on Dungeness crabs, massive infestations by nemertean crab egg predators had not been reported for any other host. Epizootic infestations in certain populations of other host species have also been seen recently (Wickham et al. 1985; Brattey et al. 1985). The purpose of this paper is to explore the recent observations of nemertean infestations and review what quantitative information exists on nemertean–crustacean interactions in the historical literature in order to address the question of whether nemertean epizootics represent a new phenomenon or are normal events in crustacean life histories.

## Literature Review

Quantitative data for prevalence and intensity of infestation by nemertean worms on crustaceans are sparse (Table 1). Often, information is available for prevalence alone without data on intensity of infestation (Hopkins 1947; Humes 1942; Vivares 1971). Conversely, there are instances where intensity of infestation is cited while prevalence is unavailable or based on observations from only an individual host crab (Kolliker 1845; Coe 1902). Several studies present more exhaustive ecological data on both prevalence and intensity of infestation by nemerteans on populations of crustacean host species. The shore crab *Hemigrapsus oregonensis* has been analyzed for infestations by *Carcinonemertes epialti* for several years in California (Kuris 1971, 1978; Roe 1979; Shields and Kuris 1983). Both Roe and Kuris found that prevalence and intensity varied with season, size, and sex of potential host specimens. Egg-bearing females carried the highest nemertean burdens and generally represent the high end of the ranges of prevalence or intensities of infestations presented in Table 1.

Roe (1979) found *Carcinonemertes epialti* on another shore crab, *Pachygrapsus crassipes*, that is sympatric with *Hemigrapsus oregonensis*, but found higher in the intertidal zone.

TABLE 1. Summary of literature pertaining to rates and intensities of infestation by nemerteans on decapod crustacean hosts (WPC = worms per crab; WPE = worms per 1000 crab eggs).

| Host species | Reference(s) | Prevalence | Intensity |
|---|---|---|---|
| *Carcinus maenas* | Kolliker 1845 | NA | 6 WPC |
| | Giard 1888 | 100% | NA |
| *Ovalipes occelatus* | Coe 1902 | 10% | 0–60 WPC |
| *Pugettia producta* | Coe 1902 | NA | 100 WPC |
| *Eriocheir japonicus* | Takakura 1910 | 1 on several | Several dozen |
| Small crab | Takakura 1910 | NA | 2 on one crab |
| *Hepatus epheliticus* | Humes 1942 | 33% | 1 WPC |
| *Portunus sayi* | Humes 1942 | 5.3% | 1 WPC |
| *Callinectes ornatus* | Humes 1942 | 67% | 3 WPC |
| *Arenaeus cribrarius* | Humes 1942 | 25% | 1 WPC |
| *Panopeus herbstii* | Humes 1942 | 20% | 3 WPC |
| *Menippe mercenaria* | Humes 1942 | 25% | 1 to several WPC |
| *Charybdis natator* | Humes 1942 | NA | 6 WPC |
| *Euphylax dovii* | Humes 1942 | <20% | 5 worms from 24 hosts |
| *Callinectes sapidus* | Humes 1942 | 15–63% | NA |
| | Hopkins 1947 | 0–100% | NA |
| | Rogers-Talbert 1948 | 37–55% | Up to 1000 WPC |
| *Pinnixa chaetopterana* | McDermott 1966 | 28.2% | NA |
| *Pinnotheres ostreum* | McDermott 1967 | 26.4% | 1–21 WPC |
| *Dromia personata* | Vivares 1971 | 31% | NA |
| *Primela denticulata* | Vivares 1971 | 12.5% | 8 WPC |
| *Macropipus depurator* | Vivares 1971 | 3% | NA |
| *Macropipus vernalis* | Vivares 1971 | 3% | NA |
| *Xantho poressa* | Vivares 1971 | 7% | NA |
| *Brachynotus sedentatus* | Vivares 1971 | 12.5% | 8 WPC |
| *Maja verrucosa* | Vivares 1971 | 1% | NA |
| *Hemigrapsus oregonensis* | Kuris 1978 | 28–57% | 0–11 WPC |
| | Roe 1979 | 27–97% | 0–115 WPC |
| | Shields and Kuris 1983 | 95.2% | 297 WPC |
| *Phylira laevis* | Bell and Hickman 1985 | To 100% | To 43 WPC |
| *Homarus americanus* | Brattey et al. 1985 | 3.6–78.7% | 1–102 WP lobster; 14 000 max. per host |
| *Cancer antennarius* | D. E. Wickham, unpubl. data | 100% | 1.56 WPE; 2300 WPC |
| *Cancer anthonyi* | R. Okasaki, pers. comm. | 98% | 0.5–1.0 WPE |
| *Cancer magister* | Wickham 1979a, unpubl. data | 80–100% | 0.15–39.6 WPE; 225–59 400 WPC; 100 000 max. per host |

TABLE 1. (*Concluded*)

| Host species | Reference(s) | Prevelence | Intensity |
|---|---|---|---|
| *Paralithodes camtschatica* | Wickham et al. 1985 | 0–100% | 0–140.1 WPE; 250 000 max. per host. |
| *Paralithodes platypus* | D. E. Wickham and A. M. Kuris, unpubl. data | 0–13% | 0–0.005 WPE |
| *Lithodes aequispina* | D. E. Wickham and A. M. Kuris, unpubl. data | 0–47% | 0–0.5 WPE |
| *Chionocetes bairdi* | D. E. Wickham and A. M. Kuris, unpubl. data | 89–100% | 3.3–68.7 WPE |

While 51.1% of egg-bearing female *Pachygrapsus crassipes* were infested by *C. epialti*, the intensity of infestation was 1.3 worms per crab. This was much lower than the 19.5 worms per crab found at the same time on egg-bearing female *Hemigrapsus oregonensis* at a prevalence of 90.4%. She found that the timing of the reproductive cycle of *Carcinonemertes epialti* was more closely matched to the seasonal reproductive cycle of *Hemigrapsus oregonensis* than to *Pachygrapsus crassipes* and concluded that *Hemigrapsus oregonensis* was the principle host for *Carcinonemertes epialti*.

Bell and Hickman (1985) surveyed several populations of the host crab *Phylira laevis* but only cited prevalence and intensity for one host population in which prevalence was 100%. They also found increasing burdens of nemerteans with increasing host size.

Brattey et al. (1985) found that the prevalence and intensity of infestations on ovigerous female lobsters (*Homarus americanus*) by *Pseudocarcinonemertes homari* ranged widely over the geographic range sampled. Prevalence ranged from 3.6% at Northumberland Strait to 78.7% at Grand Manan Island in the Bay of Fundy. Respective intensities ranged from 1.0 worms per infested host to 102.4 worms per infested host.

Several *Cancer* spp. have been found to harbor various species of *Carcinonemertes* on the Pacific coast of North America. Prevalence of infestation on ovigerous female hosts is generally high, ranging from 80 to 100% (Wickham 1979a; R. Okasaki, pers. comm.). Intensity of infestation in these host species is generally expressed as density of worms per crab eggs rather than worms per carb. Worms per crab can be estimated using host fecundity information. The mean intensities in *Cancer* spp., especially *Cancer magister*, were too high to be accurately counted on the entire host body. Also, Wickham (1979a) was the first to directly measure predation on host crab eggs by a nemertean symbiote and felt that density per unit host egg was the most appropriate measure of the worms' impact on host populations. Carcinonemertid worms have no apparent effect on the survival of nonovigerous host individuals (Scrocco and Fabianek 1970). Density of worms on the eggs of populations of the host *Cancer antennarius* and *Cancer anthonyi* ranged from 0.5 to 1.56 worms per 1000 host eggs. Populations of *Cancer magister* could be found with low worm densities (0.18 worms per 1000 crab eggs in British Columbia in 1979) but generally had the highest intensities of infestation ever reported for nemerteans symbiotic with crustacean hosts. Average density of *Carcinonemertes errans* on egg clutches of female *Cancer magister* varied widely both geographically and over time (Table 2). Projections of host egg mortality due to worm predation were made using the stage of development of host eggs and feeding rates of worms to estimate final egg mortality at the end of the host brooding period (Wickham 1979a). Projected egg mortality ranged from 3% of the eggs produced in the British Columbia population to 94% of the eggs in the central California population. Prevalence of infestation was 100% in all populations sampled with the exception of the British Columbia and Alaska populations where prevalence was approximately 80%.

TABLE 2. Density of nemerteans (worms per 1000 crab eggs) for populations of Dungeness crabs along the Pacific coast over the last 10 yr (±SD).

| Location | Season | *n* | Density | Crab egg mortality (%) |
|---|---|---|---|---|
| Central California | 1974–75 | 38 | 15.0 ± 11.7 | 61 ± 34 |
| | 1975–76 | 86 | 8.3 ± 9.5 | 39 ± 29 |
| | 1976–77 | 35 | 10.3 ± 9.7 | 40 ± 29 |
| | 1977–78 | 49 | 25.0 ± 27.1 | 70 ± 32 |
| | 1978–79 | 33 | 7.8 ± 6.5 | 64 ± 33 |
| | 1980–81 | 25 | 31.1 ± 32.6 | 94 ± 14 |
| | 1982–83 | 12 | 8.3 ± 4.0 | 49 ± 27 |
| Northern California | 1974–75 | 32 | 1.8 ± 1.8 | 10 ± 10 |
| | 1975–76 | 40 | 4.9 ± 7.7 | 26 ± 27 |
| | 1977–78 | 39 | 2.7 ± 1.2 | 23 ± 11 |
| | 1978–79 | 35 | 5.9 ± 5.0 | 39 ± 28 |
| | 1979–80 | 39 | 9.9 ± 13.2 | 40 ± 28 |
| | 1981–82 | 15 | 5.8 ± 9.3 | 30 ± 28 |
| | 1982–83 | 56 | 3.0 ± 2.9 | 22 ± 20 |
| Oregon | 1979–80 | 21 | 9.7 ± 7.0 | 81 ± 18 |
| | 1980–81 | 35 | 6.8 ± 5.3 | 48 ± 28 |
| | 1981–82 | 5 | 8.2 ± 3.9 | 66 ± 39 |
| Washington | 1975–76 | 16 | 2.3 ± 2.8 | 17 ± 15 |
| | 1978–79 | 19 | 11.1 ± 5.4 | 49 ± 23 |
| | 1979–80 | 16 | 8.7 ± 6.3 | 52 ± 21 |
| | 1980–81 | 28 | 7.9 ± 6.1 | 37 ± 22 |
| | 1983–84 | 38 | 4.9 ± 3.1 | 28 ± 20 |
| | 1984–85 | 18 | 4.3 ± 4.3 | 30 ± 15 |
| | 1985–86 | 22 | 4.3 ± 7.1 | 28 ± 29 |
| British Columbia | 1979–80 | 23 | 0.2 ± 0.2 | 3 ± 5 |
| | 1980–81 | 22 | 0.3 ± 0.3 | 3 ± 4 |
| Alaska | 1979–80 | 30 | 0.7 ± 0.8 | 9 ± 9 |

Not all of the *Cancer magister* sampled for the data displayed in Table 2 were measured for carapace width. For those that were, however, worm density could be converted to intensity of infestation by estimating the number of eggs in the host egg clutch from the size–fecundity curve in Botsford and

TABLE 3. Intensities of infestation by *Carcinonemertes errans* on *Cancer magister* expressed as worms per crab computed from worm density per crab egg on hosts measured for carapace width. Density (worms per 1000 crab eggs) and intensity (worms per crab) are listed with their respective coefficients of variation (C.V.). The correlation between average density and average intensity is $r = 0.988$ ($p < 0.001$).

| Location | Season | *n* | Density | C.V. | Intensity | C.V. |
|---|---|---|---|---|---|---|
| Alaska | 1979–80 | 30 | 0.7 ± 0.8 | 1.14 | 1393 ± 1649 | 1.18 |
| Washington | 1978–79 | 14 | 11.9 ± 6.0 | 0.50 | 21 835 ± 12 305 | 0.56 |
| | 1979–80 | 15 | 8.3 ± 6.3 | 0.76 | 15 984 ± 12 521 | 0.78 |
| | 1980–81 | 28 | 7.1 ± 5.0 | 0.70 | 12 686 ± 9570 | 0.75 |
| | 1981–82 | 42 | 12.9 ± 9.3 | 0.72 | 24 349 ± 17 938 | 0.74 |
| | 1984–85 | 18 | 4.3 ± 4.3 | 1.00 | 7307 ± 7419 | 1.02 |
| Northern California | 1977–78 | 39 | 2.7 ± 1.2 | 0.44 | 4745 ± 2286 | 0.48 |
| | 1978–79 | 35 | 5.9 ± 5.0 | 0.85 | 12 134 ± 11 020 | 0.91 |
| | 1982–83 | 56 | 3.0 ± 2.9 | 0.97 | 5053 ± 5586 | 1.11 |
| Central California | 1978–79 | 6 | 12.8 ± 8.2 | 0.64 | 14 879 ± 8810 | 0.59 |
| | 1980–81 | 11 | 35.7 ± 45.9 | 1.29 | 67 366 ± 76 162 | 1.13 |

TABLE 4. Worm density (worms per 1000 crab eggs) on Alaskan king crab *Paralithodes camtschatica* in Alaskan waters (+SD).

| Location | Date | *n* | Worm density | Egg mortality (%) |
|---|---|---|---|---|
| Cook Inlet | July 1983 | 10 | 40.8 ± 41.7 | 47 ± 40 |
| | Aug. 1983 | 9 | 88.7 ± 93.4 | 80 ± 28 |
| | Oct. 1983 | 5 | 176.4 ± 104.2 | 100 ± 1 |
| | Mar. 1984 | 10 | 0.02 ± 0.05 | 0.1 ± 0.1 |
| | Apr. 1984 | 9 | 0.01 ± 0.03 | 0.3 ± 0.4 |
| | June 1984 | 48 | 2.4 ± 4.1 | 0.8 ± 0.7 |
| | Sept. 1984 | 19 | 31.7 ± 22.7 | 59 ± 34 |
| Kodiak Is. | June 1984 | 5 | 62.9 ± 49.2 | 7 ± 9 |
| | July 1984 | 5 | 15.6 ± 8.0 | 21 ± 13 |
| | Aug. 1984 | 5 | 140.2 ± 109.1 | 97 ± 4 |
| Dutch Harbor | Oct. 1983 | 5 | 0.4 ± 0.4 | 21 ± 34 |
| | Aug. 1984 | 22 | 53.0 ± 128.1 | 35 ± 40 |
| Sand Pt. | Sept. 1983 | 15 | 0.0 | 0 |
| Norton Sd. | July 1983 | 28 | 0.0 | 0 |
| Adak Isl. | Nov. 1983 | 6 | 0.4 ± 0.5 | 3 ± 3 |

Wickham (1978). Worms per crab was the product of worms per crab egg multiplied by number of eggs. For the measured set of hosts, intensities of infestation ranged from 1393 worms per crab to 67 366 worms per crab (Table 3). The correlation of average worm density with intensity of infestation is highly significant ($r = 0.988$, $p < 0.001$), so the two measures can be freely interchanged. The coefficients of variation are similar whether density per crab or per 1000 crab eggs is used.

Measures of nemertean infestation on the Alaskan king crab (*Paralithodes camtschatica*) and tanner crab (*Chionocetes bairdi*) have been obtained in the same fashion as with *Cancer magister* (see Tables 1 and 4). A representative egg-bearing pleopod is removed from the crab's egg clutch and preserved in fixative in the field (Wickham et al. 1985). This is analyzed for the number of worms or other symbiotes and for the number of live and dead eggs or empty egg membranes. These crab species harbor populations of worms too high in number to assess total number of worms per crab, so density per crab egg is used as in *Cancer magister*.

The nemertean densities found on *Paralithodes camtschatica* cover the widest range yet measured on crabs in nature (Table 4). In certain populations and seasons, nemertean density was high enough to cause the mortality of nearly all the eggs brooded by the host crabs. In other areas, nemerteans are completely absent (Wickham et al. 1985). The study of nemertean infestations on king crabs is complicated by the presence of what appear to be as many as five different undescribed species including two probable new genera (D. E. Wickham and A. M. Kuris, unpubl. obs.).

## Discussion

The observation of massive infestations of *Carcinonemertes errans* on the crab *Cancer magister* in central California and concomitant egg mortality in the host population suggested that this source of mortality could be involved in the prolonged

collapse of the fishery for that crab population (Wickham 1979a). In 1974, when the initial observations on the central California population were begun, the still abundant crab population in northern California suffered from nemertean infestation intensities an order of magnitude lower than those in central California. Botsford and Wickham (1978) have argued that fishing pressure on *Cancer magister* could change the population structure and lead to instability in crab abundance. If the heavily exploited populations of *Cancer magister* on the Pacific coast represented "unnatural" states, it is possible that the dynamics of infestation by the nemertean *Carcinonemertes errans*, specific to *Cancer magister*, might also deviate from an unperturbed "natural" state. Just what is the natural state for the interaction between nemertean symbiotes and their crustacean hosts? This question becomes significant if we are to assume that any observation actually represents an abnormal condition.

The survey of literature pertaining to observations of nemerteans on crustaceans includes studies conducted on a wide variety of host species over a broad geographic range. The earliest observations were in European waters but quantitative information was rarely included. Kolliker (1845), who first discovered nemerteans symbiotic with crustaceans, described a single host crab, *Carcinus maenas*, with six of these worms. He gave no indication whether other hosts were assayed. Giard (1888) commented that all egg-bearing female *Carcinus maenas* he looked at were infested but gave no information on intensity of infestation.

Observations on hosts described in the literature can be broken down into crustaceans that support major commercial fisheries and those that do not. Surveying the hosts listed in Table 1, the species that support important commercial fisheries are *Cancer magister*, *Cancer anthonyi*, *Callinectes sapidus*, *Paralithodes camtschatica*, *Paralithodes platypus*, *Lithodes aequispina*, *Chionocetes bairdi*, and *Homarus americanus*. Observations on the remaining host species listed in Table 1 demonstrate generally lower prevalences and lower intensities of infestation by nemerteans than on the fished species. Even where prevelance is 100% as with the crab *Phylira laevis*, intensity of infestation is low, with 43 being the maximum number of worms obtained from an individual host. The several species of hosts surveyed by Coe (1902), Humes (1942), McDermott (1966, 1967), and Vivares (1971) all demonstrated variable prevalences, often low, and low intensities of infestation compared with the fished host species group.

Many of the intensities of infestation given in Table 1 are not directly comparable with each other. The data for the nonfished group are generally expressed as worms per host. These crabs often are smaller than the fished species of crabs and, therefore, would likely carry fewer eggs in their broods. The effect of nemertean infestation on host egg survival is directly dependent on the various worm feeding rates as well as the number of worms per crab egg. All else being equal, a smaller crab carrying a given number of worms is likely to lose a greater proportion of a brooded egg clutch to nemertean predation than a larger crab infested with the same number of worms. Most of the observations listed in Table 1 on the nonfished species display worm numbers too low to suggest that worms contribute substantial mortality to the eggs being brooded by these populations even if these crabs produce fewer eggs per clutch. Kuris (1971), studying the relatively small and unfished crab *Hemigrapsus oregonensis*, estimated a mortality rate of approximately 5% of host eggs as due to worm predation.

The crab *Cancer antennarius*, which supports only an incidental sport fishery, has been analyzed for egg mortality due to nemertean predation in one population near Santa Barbara, California. Prevalence was high (100%) and worm densities were moderately high at 1.56 worms per 1000 crab eggs (2300 per host). Predation by these nemerteans resulted in the loss of 4.7% of the eggs brooded (D. E. Wickham, unpubl. data). In the absolute numbers this represents approximately 70 000 eaten embryos per host or 30 eggs consumed per worm. Feeding rates computed for *Carcinonemertes errans* on the host *Cancer magister* are similar (70 eggs per worm) (Wickham 1979a). While only one population of *Cancer antennarius* has been assayed for egg mortality, I have never seen any instances of worm infestations on *Cancer antennarius* that result in egg mortality approaching that seen in populations of *Cancer magister*.

A good deal of quantitative information has been collected on the shore crab *Hemigrapsus oregonensis* on the California coast. Kuris (1978) found in Bodega Bay that prevalence varied seasonally from 28 to 57% on the total population but ovigerous females had rates of 45–100%. Intensity of infestation ranged from near 0 to 10 worms per host and was higher on ovigerous females ranging from about 1 to 38 worms per host. The maximum number of worms found on an individual crab was 65 on one ovigerous host and 212 on one male (although numbers such as this were rare) but usually fewer than 10 worms per host were found. Shields and Kuris (1983) discovered what appeared to be an epizootic of worms in 1983 on the population of shore crabs at the site Kuris (1978) had studied earlier. Prevalence was 95.2% and intensity was 297 worms per crab. One individual had a burden of 1680 worms. By the next spring, however, rates of nemertean infestation had dropped to levels similar to those reported earlier by Kuris (1978). Roe (1979) found generally higher burdens of nemerteans on *Hemigrapsus oregonensis* in Elkhorn Slough near Monterey Bay. Prevalence ranged from 27 to 90% with an average of 72%. Intensity of infestation ranged from 0 to 115 worms per host with an average of 14.6 worms per host. Brooding females had the highest worm burdens.

More information exists on the dynamics of infestation with commercially important crustaceans. Humes (1942) noted that prevalence of *Carcinonemertes carcinophila* on the blue crab *Callinectes sapidus* varied from 15 to 63% but gave no information on intensity of infestation. Hopkins (1947) and Rogers-Talbert (1948) measured prevalence of the same worm species on the same crab species and found that it ranged from 0% early in the summer to 100% by the end of the crabs' summer brooding period. This host appears to be a multiple brooder, producing several broods through the summer. Several generations of nemerteans are produced in a given population of hosts through the course of the summer. When a new generation of crabs moves from the estuary into coastal ocean waters where brooding occurs, they are unifested with worms. These crabs move from low-salinity water to full-salinity seawater when they mature, so it is possible that worm survival is affected by salinity. Dungeness crabs also have been found to have a higher prevalence of infestation by *Carcinonemertes errans* in ocean waters outside the Columbia River estuary in Oregon than inside the estuary where water salinities are lower (G. McCabe, pers. comm.). *Carcinonemertes errans* is sensitive to freshwater (D. E. Wickham, pers. obs.). Rogers-Talbert (1948) mentioned a maximum of 1000 worms on a crab. D. Johnson (pers. comm.) indicated that by the end of the summer in Chesapeake Bay the intensity of infestation by

worms on blue crabs is high enough to cause significant damage to host egg clutches.

The first notice of dramatically high levels of infestations by a nemertean was on the central California population of the Dungeness crab *Cancer magister* (Wickham 1978). Prevalence of infestation in that population has consistently been 100%, and the intensity of infestation has ranged from approximately 10 000 to 50 000 worms per crab (Wickham 1980; D. E. Wickham and A. M. Kuris, unpubl. data). Individual crabs can be found with more than 100 000 worms in their egg clutches. The average egg mortality has exceeded 50% in this crab population over the past 10 yr. This crab population suffered from a collapse in 1960 and has shown no indication of recovery. To date, the elevated levels of egg loss due to *Carcinonemertes errans* are the only documented source of extraordinary mortality found in this population of crabs, and high egg loss is a prime suspect in the reduction of crab abundance.

The initial observations on the central California Dungeness crab population were taken in 1974, 15 yr after the collapse of the host population, and heavy infestations by nemerteans on this population were observed but not quantified as early as 1968 (A. M. Kuris, pers. comm.). The condition in 1974 was one of high numbers of worms on a reduced number of hosts. In 1974 the northern California crab population was just moving from a period of low abundance into a resurgence of crab abundance. Over the next 10 yr the crab populations in northern California, as well as in Oregon and Washington, reached high levels with a peak in 1976 followed by a decline in the early 1980's. This continued a cyclic pattern of abundance that has typified these fisheries for the last 40 yr. Botsford and Wickham (1978) suggested that changes in the age structure of these populations brought about by the fishery could cause or exacerbate fluctuations in abundance. Nemertean density in the northern California crab population in 1974 was an order of magnitude lower than that in central California, although prevalence was 100% in both regions. In 1974, egg loss in the northern California Dungeness crab population was approximately 10% compared with a 61% loss in the central California population.

The data shown in Table 2 show that nemertean abundance in northern California, Oregon, and Washington increased and that crab-egg mortality approached that found in central California. Over the past few years the nemertean epizootic in the north has begun to abate and densities have lowered somewhat.

Wickham (1979b) proposed a model to show how periodic peaks of host abundance could lead to persistent epizootics of *Carcinonemertes errans*, which appears to be the case in central California. The central California Dungeness crab fishery began to be exploited at near maximum intensity at least 20 yr prior to the heavy exploitation of the northern fisheries. The central California fishery fluctuated in abundance in a pattern similar to that found later to the north and achieved record landings in 1957 after which it collapsed and still has not recovered. No historical data on worm density exist prior to 1968. The increase in worm density in northern California in response to the peak of crab abundance suggests that a similar epizootic may have occurred after the record crab abundances in the 1950's in central California. The epizootic in central California, however, has persisted.

Nemertean densities on Dungeness crabs in British Columbia are the lowest seen on this host species. Prevalence is also lower, being only 80%. This fishery has only recently been conducted at a high exploitation rate and does not cycle (Jamieson 1985). Dungeness crabs from Alaska sampled in 1979 were infested by *Carcinonemertes errans* with prevalences and intensities similar to those found in the British Columbia crab population. Exploitation rates in the Alaska Dungeness crab fishery are nearly as high as in California, Oregon, or Washington but this crab population has been exploited for only 20 yr at this rate compared with 40 yr in the other fisheries. The Alaska catch record is now beginning to demonstrate cyclic behavior and is worth observing in the future to see if the pattern of abundance achieves the regularity of cycling seen in northern California, Oregon, and Washington. Nemertean infestation rates would be expected to oscillate with crab abundance as they appear to do elsewhere.

*Cancer anthonyi* is currently under study in Santa Barbara and also harbors a species of nemertean (R. Okasaki, pers. comm.). Approximately 98% of the egg clutches sampled were infested and worm density appears to range from 0.5 to 1.0 worms per 1000 crab eggs. Total egg mortality attributable to nemerteans is under 10%. This *Cancer* crab supports a new and growing commercial fishery in southern California.

Two more crustacean species have recently come under study because of what appears to be significant new observations of extensive egg mortality. The first is the American lobster *Homarus americanus* which is known to harbor the recently described nemertean *Pseudocarcinonemertes homari* (Fleming and Gibson 1981). Research in Canadian waters has shown that in certain locations the prevalence of infestation can be as high as 78% (Brattey et al. 1985). The intensity of infestation ranged up to 102 worms per ovigerous lobster. As with *Carcinonemertes* spp., *Pseudocarcinonemertes homari* concentrates on egg-bearing hosts. It is difficult to compare directly the effect of *Pseudocarcinonemertes homari* on lobster egg mortality with crab egg mortality caused by worms. Lobsters display extensive grooming behavior on their eggs. Aiken et al. (1985) found that certain lobsters infested with *Pseudocarcinonemertes homari* would strip the egg-bearing pleopods of worms and eggs. This behavior means that lobsters that remove broods infested by nemerteans suffer total brood loss, even though the worms might have destroyed a much smaller portion of the egg clutch through direct feeding. This behavior confounds efforts at achieving an accurate assessment of total egg mortality caused by *Pseudocarcinonemertes homari* in natural populations. Some female lobsters will have lost eggs to egg predation and to the concomitant stripping behavior; however, since the worms would no longer be present on the lobsters at the time of possible sampling for study, the lack of a brood on those animals could be attributed to factors other than nemertean predation, for instance infertility due to lack of insemination. It is curious that an animal as well studied as the American lobster should only recently be discovered to harbor such large numbers of nemerteans. These nemerteans appear to be well adapted to their hosts, and it is likely that they have been associated with lobsters for a long time. It is possible that nemertean densities have only recently increased to the point where they become obvious, as appears to be the case with worms from *Cancer magister* and *Paralithodes camtschatica*.

With *Cancer* spp. the membranes of eggs eaten by nemerteans remain attached to the pleopods and worms remain in the host egg clutch until either all the eggs are consumed by the worms or the host eggs hatch. Wickham (1979a) found that *Carcinonemertes errans* was virtually the only source of egg mortality in natural host populations and that the predation is obvious and can be quantified and followed through the brood

period. This is clearly not the case with the American lobster.

Researchers from the Alaska Department of Fish and Game noticed in 1982 a dramatic decline in the survival of eggs of the red king crab *Paralithodes camtschatica*. Preserved crab egg samples demonstrated massive infestations with species of nemerteans (Wickham et al. 1985). Subsequent research has shown the complexity of obtaining an accurate assessment of the impact of nemerteans on this host. Seasonal samples at both Kodiak Island and Homer show that the species of nemertean on king crabs in those locales only appears to utilize a small portion of the host's 11-mo brood period (Table 4). Red king crabs deposit their egg clutches in April or May and brood the eggs until the next February or March. Egg samples are free of nemerteans and demonstrate no egg mortality until June or July when large numbers of worms are first found in these samples. Egg mortality is low at first but proceeds rapidly through the summer until by fall several king crab populations suffer from the destruction of virtually all their eggs. After destruction of the host egg clutch the worms leave. It is not clear whether this is a normal seasonal emigration or whether this is limited to crabs that have lost all their eggs. In order to accurately quantify egg predation rates in king crab populations in nature, it is important to sample throughout the brooding period of the hosts.

The situation with Alaskan king crabs shares some similarities with that seen in the Pacific coast Dungeness crabs. Both of these species have supported enormous fisheries and both have suffered from dramatic fluctuations in abundance with some populations declining to persistent low levels. The populations that are persistently low also harbor some of the highest nemertean densities and suffer from high egg loss. The two major fisheries for the red king crab historically have been the Kodiak fishery and the Bristol Bay fishery in the Bering Sea. During the 1960's, Kodiak contributed the major share of crabs caught in the state's waters, but catches declined to low levels in 1970. A small upturn occurred later in the 1970's but not to levels comparable with the earliest peak of abundance. No historical data exist on nemertean abundance prior to 1982; however, gross observations on egg clutches were taken from the 1940's to 1968 (Powell and Lebida 1968). Prior to 1960 the percentage of crabs not brooding full clutches of eggs during the brood season was virtually zero. During the 1960's the percentage of nonbrooding females began to increase until in certain populations in 1968 as many as 29% of the female crabs had no eggs. Their survey only took note of crabs with a complete absence of eggs. Egg mortality, however, can occur in crabs still carrying what to the naked eye appear to be full egg clutches. Accurate measurement of egg mortality can be obtained only through microscopic observation. The overall egg mortality at the time of their study could have been considerably higher. No mention was made of nemertean presence; however, these worms are small and generally the same color as the eggs and often have been missed by untrained observers, or not looked for at all.

The Bristol Bay king crab fishery provided the bulk of the catches from Alaska during the 1970's. This fishery collapsed in the 1980's. Nemerteans have been found in this population also but appear to be a different species. Worms on king crabs from the Gulf of Alaska are small (1–2 mm as adults) and have the usual two eyes of *Carcinonemertes* spp. The nemerteans found on crabs from the Alaskan Peninsula, the Aleutians, and the Bering Sea are large (20–30 mm as adults) and have no eyes. They probably represent an undescribed different species and possibly a new underscribed genus. The densities of these large worms are lower and egg mortality of the crabs in the Bering Sea is lower than in the Gulf of Alaska. This suggests that the collapse of the host population is not due to nemertean predation. The dynamics of the relationship between nemerteans and Dungeness crabs indicate that crab populations can fluctuate for reasons other than nemertean predation. If problems exist with egg predation by nemertean worms, it may be that heavy infestations of nemerteans prevent recovery of collapsed host populations.

The king crab fishery is beginning to shift to two other species of crab now that *Paralithodes camtschatica* abundance has declined. These are the blue king crab *Paralithodes platypus* and the golden king crab *Lithodes aequispina*. Both of these species harbor nemerteans, but prevalences are very low and intensities are also low (Table 1). Many uninfested populations of these species exist which exhibit virtually no egg mortality.

Epizootic infestations of nemertean egg predators exist on certain host species, and while we still lack a broad perspective on nemertean–crustacean interactions, a few general observations can be made. In populations of the extensively studied crab *Cancer magister*, prevalence and intensity of infestations appear to be higher in populations that have supported a maximum-effort fishery for proportionally longer time periods. This also appears to be the case when comparing infestations in two other *Cancer* spp., *Cancer anthonyi*, which has only begun to support an intensive commercial fishery, and *Cancer antennarius*, which is subject to very little fishing pressure. The same observation can be made with the king crab species in Alaska. The king crab that has been fished the most heavily and for the longest period is *Paralithodes camtschatica*. It suffers from much more intense nemertean infestations than *Paralithodes platypus* or *Lithodes aequispina*, both of which are just now beginning to be heavily exploited. The heavily fished crab species *Callinectes sapidus* is an interesting exception to the above examples. Prolonged epizootics have never been described in this species. Instead, nemertean abundance reaches relatively high levels every year. This, however, happens only late in the summer after the population has been able to complete much of its egg production. Blue crabs, by utilizing freshwater for the early portion of their life history, may be provided a unique escape from nemertean epizootics unavailable to crabs that lead an entirely marine existence.

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## References

AIKEN, D. E., S. L. WADDY, AND L. S. UHAZY. 1985. Aspects of the biology of *Pseudocarcinonemertes homari* and its association with the American Lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 351–356.

BELL, P. J., AND J. L. HICKMAN. 1985. Observations on *Carcinonemertes* (Nemertea: Carcinonemertidae) associated with the smooth pebble crab, *Phylira laevis*. Pap. Proc. R. Soc. Tasmania 119: 65–68.

BOTSFORD, L. W., AND D. E. WICKHAM. 1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35: 833–843.

BRATTEY, J., A. CAMPBELL, A. E. BAGNALL, AND L. S. UHAZY. 1985. Geo-

graphic distribution and seasonal occurrence of the nemertean *Pseudocarcinonemertes homari* on the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 360–367.

COE, W. R. 1902. Nemertean parasites of crabs. Am. Nat. 36: 431–450.

FLEMING, L. C., AND R. GIBSON. 1981. A new genus and species of monostiliferous hoplonemerteans, ectohabitant on lobsters. J. Exp. Mar. Biol. Ecol. 52: 79–93.

GIARD, A. 1888. Le Labortoire de Wimereux en 1888. (Recherches fauniques.) Bull. Sci. France Belg. 19: 492–513.

HOPKINS, S. H. 1947. The nemertean *Carcinonemertes* as an indicator of the spawning history of the host *Callinectes sapidus*. J. Parasitol. 33: 146–150.

HUMES, A. G. 1942. The morphology, taxonomy, and bionomics of the nemertean genus *Carcinonemertes*. Ill. Biol. Monogr. 18: 1–105.

JAMIESON, G. S. 1985. Dungeness crab, *Cancer magister*, fisheries of British Columbia, p. 37–60. *In* B. R. Melteff [ed.] Proceedings of the Symposium on Dungeness Crab Biology and Management. Lowell Wakefield Fish. Symp. Ser., Alaska Sea Grant Rep. 85-3.

KOLLIKER, A.VON. 1845. Ueber drei neue Gattungen von Wurmen, Lineola, Chloraima, Polycystia, neue Wurgattungen und neue Arten von Nemertes. Verh. Schweiz. Naturforsch. Ges. Chur. 29: 86–98.

KURIS, A. M. 1971. Population interactions between a shore crab and two symbionts. Ph.D. dissertation, University of California, Berkeley, CA.

1978. Life cycle, distribution, and abundance of *Carcinonemertes epialti*, a nemertean egg predator of the shore crab, *Hemigrapsus oregonensis* in relation to host size, reproduction and molt cycle. Biol. Bull. 154: 121–137.

MCDERMOTT, J. J. 1966. The biology of a nemertean parasite of pinnotherid crabs. Am. Zool. 6: 331.

1967. The oyster crab, *Pinnotherum ostreum*, as a host for a parasitic nemertean. Am. Zool. 7: 772–773.

POWELL, G. J., AND LEBIDA. 1968. Egg production success of Alaskan king crabs collected from the Aleutians, Kodiak Island, and lower Cook Inlet, 1938–1968. Alaska Department of Fish and Game, King Crab Staff Report. 6 p.

ROE, P. 1979. Aspects of development and occurrence of *Carcinonemertes epialti* (Nemertea) from shore crabs in Monterey Bay, California. Biol. Bull. 156: 130–140.

ROGERS-TALBERT, R. 1948. The fungus *Lagendium callinectes* Couch (1947) on eggs of the blue crab in Chesapeake Bay. Biol. Bull. 94: 214–228.

SCROCCO, V. M., AND J. FABIANEK. 1970. Biological relationship of *Callinectes sapidus* (Rathbun) with carcinonemerteans, bryozoans, and barnacles. Proc. Soc. Exp. Biol. Med. 133: 299–302.

SHIELDS, J., AND A. M. KURIS. 1983. An epidemic of *Carcinonemertes epialti* in an unfished population of *Hemigrapsus oregonensis*. Am. Zool. 23: 924.

TAKAKURA, U. 1910. Kisei himomushi no ishi Shinsu. (On a new species of parasitic nemertean.) Dobutsugaku Zasshi 22: 111–116.

VIVARES, C. P. 1971. Parasites de Crustaces Decapodes. Ann. Parasitol. Hum. Comp. 46: 1–9.

WICKHAM, D. E. 1978. A new species of *Carcinonemertes* (Nemertea: Carcinonemertidae) with notes on the genus from the Pacific coast. Proc. Biol. Soc. Wash. 91: 197–202.

1979a. Predation by *Carcinonemertes errans* on eggs of the Dungeness crab, *Cancer magister*. Mar. Biol. 55: 45–53.

1979b. The crab egg predator *Carcinonemertes errans* and cycling and collapse of crab populations. Ph.D. dissertation, University of California, Berkeley, CA. 91 p.

1980. Aspects of the life history of *Carcinonemertes errans* (Nemertea: Carcinonemertidae), an egg predator of the crab *Cancer magister*. Biol. Bull. 159: 247–257.

WICKHAM, D. E., S. F. BLAU, AND A. M. KURIS. 1985. Preliminary report on egg mortality in Alaskan king crabs caused by the egg predator *Carcinonemertes*, p. 265–270. *In* Proceedings of the International King Crab Symp. Ser., Alaska Sea Grant Rep. 85-12.

# Influence of Light and Food on Larval American Lobsters, *Homarus americanus*

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Eagles, M. D., D. E. Aiken, and S. L. Waddy. 1986. Influence of light and food on larval American lobsters, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2303–2310.

Survival, size, and rate of development of larval American lobsters, *Homarus americanus*, to fourth stage are correlated postively with food quality. High survival requires that first-stage larvae encounter an abundance of food. Larval survival was higher in low light intensity than in a higher intensity that was well below that of full sunlight. Larvae reared on LD 12:12 photoperiods molted to the fourth stage predominantly during the dark phase, even when the timing of the light and dark phases was reversed. Larvae reared in continuous darkness developed faster and were almost twice the weight of larvae reared in a LD 12:12 photoperiod, but fewer survived to fourth stage.

La survie, la taille et la vitesse de développement des larves de homard américain, *Homarus americanus*, jusqu'au quatrième stade présentent une corrélation positive avec la qualité de la nourriture. Pour que la survie soit forte, il faut que les larves de premier stade bénéficient d'une nourriture abondante. La survie des larves était plus élevée sous un faible éclairement que sous un éclairement plus fort, qui restait toutefois nettement au-dessous de celui du plein soleil. Les larves élevées avec une photopériode de douze heures de lumière et douze heures d'obscurité connaissaient généralement leur mue du quatrième stade pendant la phase obscure, même en cas d'inversement des phases de lumière et d'obscurité. Les larves élevées dans l'obscurité constante se développaient plus vite et pesaient presque deux fois plus que les larves élevées avec photopériode 12:12, mais étaient moins nombreuses à survivre jusqu'au quatrième stade.

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Larval survival is a critical factor in lobster recruitment and is thought to be controlled mainly by food limitation, temperature, and predation (see Phillips and Sastry 1980; Harding et al. 1983). Unfortunately, little is known about larval development in the wild and we are dependent on laboratory studies for information. Although survival, growth, and development rates in captivity may be different from those in the wild, studies conducted under culture conditions have demonstrated the relative effects of environmental factors such as nutrition, oxygen, salinity, season, light, and photoperiod (Aiken et al. 1981, 1982; Carlberg and Van Olst 1976; Ford et al. 1979; Hadley 1906; Huntsman 1924; Templeman 1936). Recent attempts to standardize methods for rearing lobster larvae have been complicated by the effects of daylength, season, and food on survival, growth, and development (Aiken et al. 1981, 1982).

The present study extends earlier observations on the effects of light and demonstrates the impact of food quantity and quality on survival, growth, and development of larval *Homarus americanus*.

## Methods

### General Methods

Larvae were reared in a flow-through water system using 40-L planktonkreisels ("pots") enclosed in lightproof cabinets (Aiken et al. 1981). Seawater (salinity 28–31‰) was filtered with No. 2 silica sand and supplied at 20 ± 0.5°C to all pots at 2–4 $L \cdot min^{-1}$ from a common reservoir.

The light source was a Westinghouse 15-W F15T8/CW fluorescent bulb, suspended 30 cm above the water in each cabinet. The bulb was encased in a clear acrylic sheet to reduce condensation. Light intensity was reduced by centering a sheet of opaque plastic between the bulb and acrylic sheet. The appropriate amount of light was admitted through a narrow slit in this sheet. The spectrum of this bulb showed major peaks at 440 and 580 nm. Light intensity at the water surface was 0.31 and 0.15 $W \cdot m^{-2}$ (at 440 and 580 nm, respectively) measured with a "Li-Cor" model IL700 radiometer/photometer. A LD 12:12 (06:00–18:00) photoperiod was used in all experiments and was controlled with Intermatic T-109 time clocks.

Ovigerous lobsters were obtained from the Bay of Fundy and were held at local temperature (varying 0–14°C annually) and then 20°C to achieve hatching at the required time (Aiken and Waddy 1985). The one exception was the lobster that hatched in September. Embryonic development on this lobster was extended by 2 mo with low temperature (6°C) during the 5 mo prior to hatch.

Within each experimental group, pots were stocked in the morning of one day with 1000 newly hatched sibling first-stage

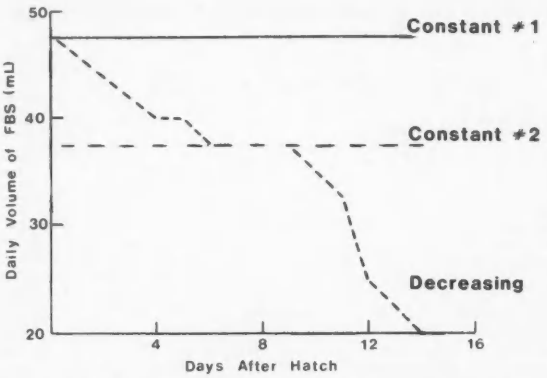


FIG. 1. Total quantity of adult brine shrimp (*Artemia*) fed daily. With two schedules the feeding rate was kept constant throughout development, while the amount fed in the third schedule decreased throughout development and ranged from 47.5 to 20 mL·d$^{-1}$

lobster larvae. Larvae were fed commercially available San Francisco Bay Brand frozen brine shrimp (FBS). The FBS was thawed and diluted 1:1 with seawater and introduced to the pots through lightproof tubes in the cabinets at 08:00, 12:00, and 16:00 daily.

Fourth-stage larvae were removed from the pots twice daily, just after the lights came on (06:00−06:30) and just before the lights went out (17:30−18:00). The harvested larvae from each pot were dried as a group to a constant weight for 10−12 h at 70°C and weighed to the nearest milligram.

Survival and time of molt comparisons were done using an adjusted chi square (Steel and Torrie 1960) and a Brownlee proportion analysis (Brownlee 1960). Mean weights were compared using a *t*-test for unpaired data and an *F*-ratio for their variance. Weight measurements from samples of fewer than five larvae from a single pot or the appropriate multiple for combined runs were not considered statistically valid and were excluded from the comparisons. Time to 80% metamorphosis was calculated using probit analysis (Finney 1952).

Due to the harvesting technique used, a statistical comparison of the development rates was not possible. A 10% difference in development time to fourth stage arbitrarily was chosen to be significant.

### Experiment 1. Food Quantity ($N$ = 12 000)

This experiment was conducted in March and repeated in May 1984. In each, there were two replicates of three feeding regimes each with 1000 larvae. In two of the regimes, larvae were fed equal amounts each day, with one group receiving 47.5 mL and the other 37.5 mL of thawed FBS per 1000 stage I larvae (before dilution) per day (Fig. 1). In the third regime, larvae were fed less brine shrimp in the later stages than during early development, with 47.5 mL of FBS fed on the first day, decreasing to 20 mL by day 14 (Fig. 1).

### Experiment 2. Reversed Photoperiod ($N$ = 10 000)

This experiment was conducted in June and repeated in August 1983. Photoperiod was LD 12:12, and for larvae fed during the dark, the hours of night and day were reversed. First-stage larvae were placed directly into the phase, either light or dark, in which they were to be fed.

In June, three replicates of 1000 larvae each were fed during the light phase and one group (1000 larvae) was fed during the dark phase. In August, three replicates of 1000 each were fed in each phase. All groups were fed on a decreasing schedule as described above.

### Experiment 3. Food Quality ($N$ = 17 000)

This experiment was repeated four times between September 1983 and March 1984. Three lots of FBS obtained over a few months from one supplier were used as food. Brine shrimp were stored at −90°C until use. One lot contained intact red brine shrimp, while another had mostly fragmented brine shrimp (Fig. 2). The third lot, although the brine shrimp were intact, was pale and had a lower carotenoid content than the other lots (Fig. 3). These three types of brine shrimp were subjectively classified as "normal", "fragmented", and "pale". Carotenoids were extracted from each type of brine shrimp and from fourth-stage lobster larvae reared on each type, according to the method of D'Abramo et al. (1983). Absorbance was measured with a Bausch & Lomb Spectronic 2000 at an absorption maximum of 471 nm. The quantity of pigment in the brine shrimp was determined using the extinction coefficient for canthaxanthin (Krinsky 1965). For lobster larvae the extinction coefficient for astaxanthin was used.

In the first group (September), three replicates of 1000 larvae each were fed pale brine shrimp and three replicates of 1000 larvae each were fed fragmented brine shrimp. Two groups were run in January. In the first, 1000 larvae were reared on each of the three types of brine shrimp. In the second January group, only two types of FBS were used: fragmented and normal brine shrimp (one pot each). In March, three replicates of 1000 larvae each were fed pale brine shrimp, and three replicates of 1000 larvae each were fed the normal brine shrimp.

### Experiment 4. Light Intensity ($N$ = 12 000)

The first phase of this experiment compared the effect of high and low light intensity on larval development. Low light intensity was that used in previous experiments and high light intensity was obtained by removing the opaque plastic sheet from the fluorescent lamp. This increased the light intensity 30 times to 9.38 W·m$^{-2}$ at 440 nm and 4.72 W·m$^{-2}$ at 580 nm. The experiment was repeated five times as follows: March 1983: 1000 larvae, full intensity and 1000 larvae, low intensity; May 1982: 1000 larvae, full intensity; May 1983: two replicates (1000 larvae each), low intensity; July 1982: 1000 larvae, full intensity; July 1984: three replicates (1000 larvae each), low intensity.

The second phase of the experiment compared the effects of rearing larvae in continuous dark (DD) versus a LD 12:12 photoperiod under low light intensity. The two groups in this experiment were as follows: May 1984: two replicates (1000 larvae each) LD 12:12, 1000 larvae DD; June 1984: three replicates (1000 larvae each) LD 12:12, 1000 larvae DD.

## Results

### Experiment 1. Food Quantity

*Group 1: March*

Larvae on all three feeding regimes developed to fourth stage at the same rate and weighed the same at fourth stage (Table 1).

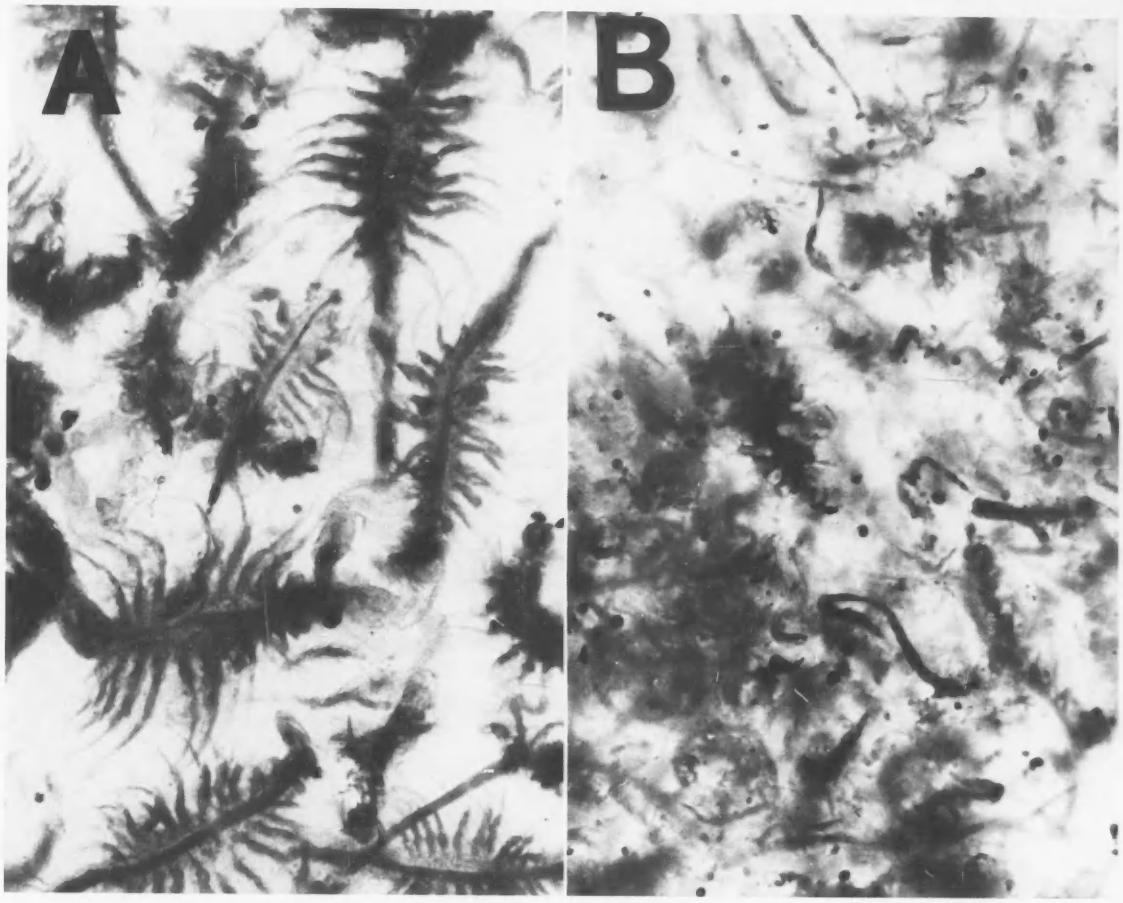


FIG. 2. Variation in integrity of frozen adult brine shrimp (*Artemia*) available from a commercial supplier. (A) Shipment with a high percentage of intact individual brine shrimp; (B) shipment with a high percentage of broken or fragmented brine shrimp.

However, survival was affected by the feeding regime. Those fed 47.5 $mL \cdot d^{-1}$ survived significantly better than those fed 37.5 $mL \cdot d^{-1}$ (Table 1). But when the 37.5 $mL \cdot d^{-1}$ was fed in greater amounts during the first stage and lesser amounts during the second and third stages (beginning with 47.5 $mL \cdot d^{-1}$ and decreasing to 20 $mL \cdot d^{-1}$ by day 14), survival was improved (39.5 vs. 34.3%, $p < 0.05$).

Most of the larvae in the experiment molted to fourth stage during the dark phase. A significantly greater percentage of larvae on the decreasing feeding regime molted during the dark (85.7%) than on the other feeding regimes (80.2 and 82.6%) (Table 1).

*Group 2: May*

When the experiment was repeated in May, there were no differences in survival, weight, development rate, or time of molt between the three feeding regimes (Table 1).

## Experiment 2. Reversed Photoperiod

In both the June and August groups, survival was higher ($p < 0.01$) in larvae fed during the dark phase (Table 2). However, when data from the two months were pooled, the larger sample size and variability between groups made the difference insignificant. Weight of dark-fed larvae was not significantly different from weight of light-fed larvae, but dark-fed larvae took longer to reach fourth stage (21.3 vs. 19.5 d) (Table 2).

Molting to fourth stage occurred primarily during the dark phase in both light- and dark-fed regimes, although more dark-fed larvae molted in the dark (89.8 vs. 81.7%, $p < 0.005$) (Table 2).

## Experiment 3. Food Quality

The normal brine shrimp diet produced the highest survival to fourth stage, greatest weight, and shortest development time of the three diets. In contrast, the fragmented brine shrimp diet produced the lowest survival, lowest weight, and longest development time (Table 3).

Although the pale brine shrimp produced survival equivalent to that from the normal diet, weight was significantly reduced and development time was extended (Table 3). In addition, fourth-stage lobsters were light yellow rather than the normal dark brown color and had a high incidence of cheliped loss:

TABLE 1. Effect of quantity of frozen brine shrimp fed to larval lobsters. Two feeding regimes fed consistent amounts each day, 37.5 and 47.5 mL·d$^{-1}$.The decreasing feeding regime provided decreasing amounts during development (ranging from 47.5 to 20 mL·d$^{-1}$) to adjust for larval mortality. *$p < 0.05$, **$p < 0.01$. Additional statistical comparisons for March: survival 1 vs. 3 ($p < 0.05$); % molting in the scotophase 1 vs. 3 ($p < 0.05$).

| | Feeding regime | | | | | |
|---|---|---|---|---|---|---|
| | Decreasing 1 | | 37.5 mL·d$^{-1}$ 2 | | 47.5 mL·d$^{-1}$ 3 | |
| March | | | | | | |
| Stage I larvae (*N*) | 2000 | | 2000 | | 2000 | |
| Survival (%) | 39.5±2.40 | * | 34.3±1.30 | ** | 42.8±1.35 | |
| Mean dry weight (mg) of stage IV lobsters | 5.5±0.05 | | 5.6±0.05 | | 5.6±0.05 | |
| Days to stage IV | 16.9±0.15 | | 17.4±0.90 | | 16.7±0.60 | |
| % of larvae molting to stage IV in the scotophase | 85.7±2.98 | * | 80.2±2.45 | | 82.6±2.1 | |
| May | | | | | | |
| Stage I larvae (*N*) | 2000 | | 2000 | | 2000 | |
| Survival (%) | 68.4±2.65 | | 67.0±1.10 | | 69.0±1.95 | |
| Mean dry weight (mg) of stage IV lobsters | 6.0±0.02 | | 6.1±0.00 | | 6.4±0.06 | |
| Days to stage IV | 13.4±0.05 | | 13.2±0.00 | | 13.1±0.05 | |
| % of larvae molting to stage IV in the scotophase | 88.0±2.20 | | 89.3±2.66 | | 89.6±0.86 | |

TABLE 2. Effect of feeding lobster larvae during the dark and light phase. Statistical comparisons: survival in June, light vs. dark ($p < 0.01$); survival in August, light vs. dark ($p < 0.01$); % molting in the scotophase, light vs. dark (June and August combined) ($p < 0.01$).

| | Light fed | | | Dark fed | | |
|---|---|---|---|---|---|---|
| | June | August | Pooled | June | August | Pooled |
| Stage I larvae (*N*) | 3000 | 3000 | 6000 | 1000 | 3000 | 4000 |
| Survival (%) | 26.3±2.51 | 19.1±0.75 | 22.7±4.30 | 31.0 | 21.8±2.60 | 24.0±5.07 |
| Mean dry weight (mg) of stage IV lobsters | 5.4±0.23 | 5.2±0.40 | 5.3±0.34 | 4.8 | 5.0±0.33 | 5.1±0.24 |
| Days to stage IV | 19.9±1.42 | 18.5±0.15 | 19.5±1.18 | 19.3 | 21.9±1.75 | 21.3±1.75 |
| % of larvae molting to stage IV in the scotophase | 82.4±3.91 | 80.3±1.46 | 81.7±2.82 | 95.4 | 87.2±2.05 | 89.8±4.51 |

TABLE 3. Effect of frozen brine shrimp quality on development of lobster larvae. The normal FBS was intact and dark red-brown in color. Pale FBS contained intact adults which were light brown and low in carotenoids. The fragmented FBS was dark red-brown but contained few adults. *$p < 0.05$, **$p < 0.01$. Additional statistical comparisons: survival 1 vs. 3 ($p < 0.01$; weight 1 vs. 3 ($p < 0.01$); % molting in the scotophase 1 vs. 3 ($p < 0.01$).

| | Normal FBS 1 | | Pale FBS 2 | | Fragmented FBS 3 | |
|---|---|---|---|---|---|---|
| Stage I larvae (*N*) | 5000 | | 7000 | | 5000 | |
| *Artemia* carotenoids (mg·100 g$^{-1}$) | 11.2 | | 6.8 | | 12.5 | |
| Carotenoids stage IV lobsters (mg·100 g$^{-1}$) | 1.02 | | 1.80 | | 0.76 | |
| Survival (%) | 35.8±5.26 | | 34.6±2.60 | ** | 20.1±7.59 | |
| Mean dry weight (mg) of stage IV lobsters | 6.2±0.26 | ** | 5.4±0.17 | * | 5.2±0.22 | |
| Days to stage IV | 14.8±0.61 | | 16.0±1.50 | | 17.6±0.40 | |
| % of larvae molting to stage IV in the scotophase | 74.2±10.93 | ** | 58.7±7.45 | ** | 88.2±3.08 | |

60% of a subsample of fourth-stage larvae ($N = 511$) were missing one or both claws as compared with only 10% of larvae ($N = 456$) fed normal brine shrimp. Also, many of the pale larvae did not complete the molt to fourth stage and still had the old shell attached.

The pale brine shrimp had only 61% of the carotenoids found in the normal brine shrimp and produced fourth-stage lobsters with an astaxanthin content 25.5% lower than those fed normal brine shrimp (Table 3).

Most larvae fed normal (74.2%) and fragmented brine

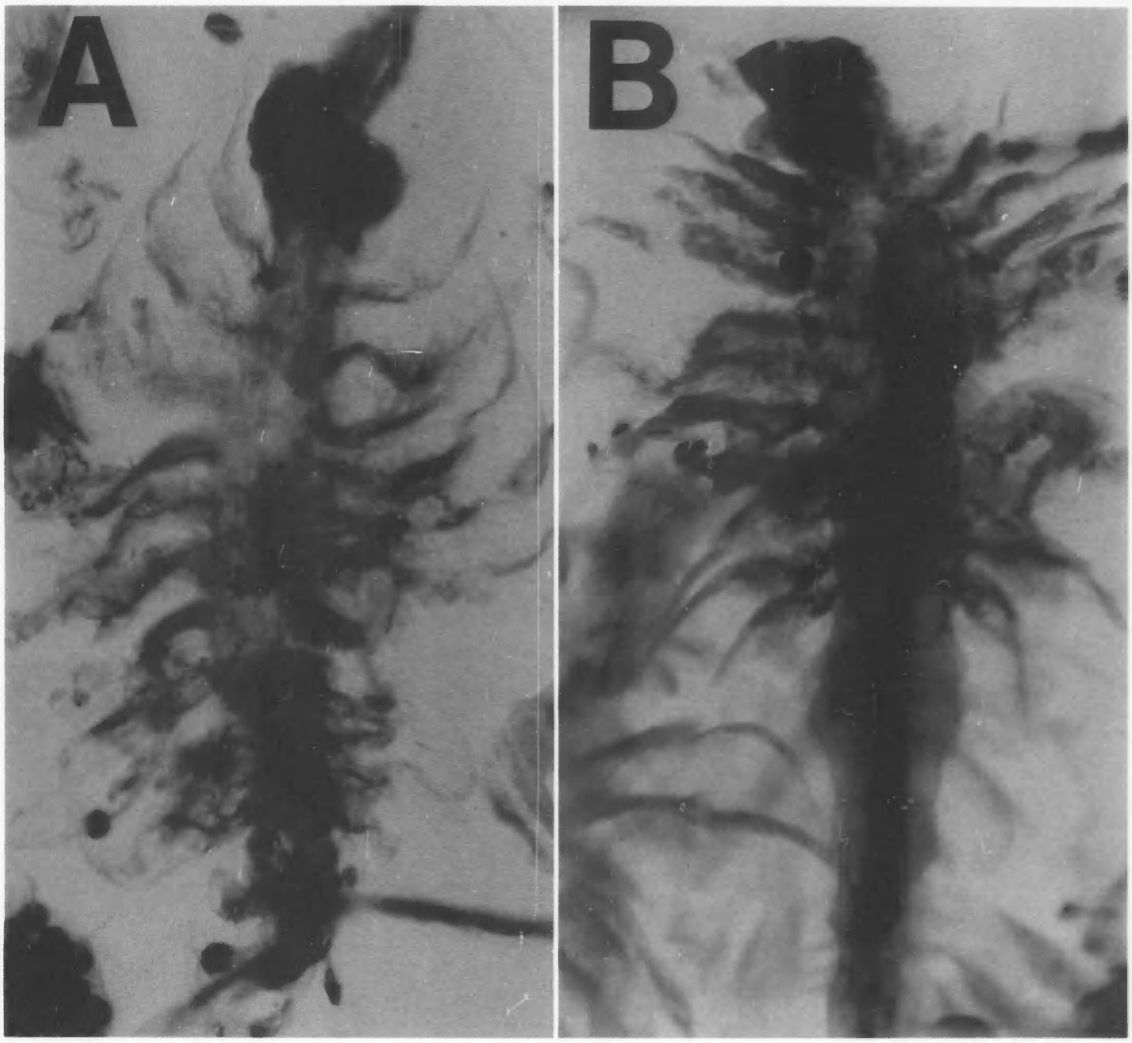


FIG. 3. Variation in pigmentation of frozen adult brine shrimp (*Artemia*) available from a commercial supplier. (A) Pale colored brine shrimp; (B) normal red-brown pigmented brine shrimp.

TABLE 4. Effect of light intensity on lobster larval development. The energy levels at the surface for the 440-nm wavelength were 9.38 and 0.31 $W \cdot m^{-2}$ for the high and low intensity, respectively. $*p < 0.05$, $**p < 0.01$.

| | March | | May | | June | |
|---|---|---|---|---|---|---|
| | High | Low | High | Low | High | Low |
| Stage I larvae ($N$) | 1000 | 1000 | 1000 | 2000 | 1000 | 3000 |
| Survival (%) | 44.6 ** | 50.7 | 29.8 ** | 40.0±1.20 | 39.3 ** | 44.8±1.06 |
| Mean dry weight (mg) at stage IV | 6.3 | 6.4 | 4.6 * | 5.7±0.15 | 4.6 * | 6.6±0.06 |
| Days to stave IV | 14.3 | 14.3 | 15.2 | 14.8±0.40 | 15.8 | 14.6±0.26 |

shrimp (88.2%) molted in the dark, but larvae fed pale brine shrimp showed little tendency to molt in the dark (58.7%, $p < 0.05$).

Experiment 4. Light Intensity

Low light intensity produced significantly better survival than high light intensity, but there were no differences in development time (Table 4). In May and July, mean weight was significantly greater for larvae reared in low light intensity.

Larvae reared in the dark (DD) were significantly heavier than larvae reared under a LD 12:12 photoperiod, but their survival was significantly lower (Table 5). Development time in the dark could not be calculated, as larvae could not be harvested until the cabinets were opened. Harvest day used the the DD group in May (day 15) yielded only fourth-stage larvae. On harvest day for the DD group in June (day 14), 98.4% of the larvae were fourth stage, as compared with 84.1% from the LD 12:12 group.

## Discussion

Larval survival was improved by increasing the amount of FBS fed each day from 37.5 to 47.5 $mL \cdot d^{-1}$. However, by changing the amount fed during development to reflect the number of surviving larvae, total survival was also increased. Larvae fed amounts decreasing from 47.5 $mL \cdot d^{-1}$ on day 1 to 20 $mL \cdot d^{-1}$ by day 14 survived better than larvae fed 37.5 $mL \cdot d^{-1}$, even though the total amount fed was identical in each case. Survival further increased when the greater amount (47.5 $mL \cdot d^{-1}$) was fed throughout development, although the rate of development remained the same. In contrast, those receiving less food (37.5 $mL \cdot d^{-1}$) took longer to reach fourth stage (Table 1). These results indicate that food availability is especially important immediately after hatch and that quantity will affect both survival and rate of development. In these studies, the amounts of food provided did not vary enought to affect weight at fourth stage, suggesting that weight is related to the total amount of food available during development and not to that available at certain stages during development.

The differences in survival and development rate obtained in March were not obtained when the study was repeated in May (Table 1). Consistent with previous results at that time of year, development was rapid (13.2 d), suggesting that season or embryonic history modified the results. We have no explanation for this apparent seasonal effect, but differences in yolk reserves between eggs developed at different temperatures is a possibility (see Anger et al. 1985; Sasaki et al. 1986).

TABLE 5. Effect of rearing lobster in total darkness. $*p < 0.05$, $**p < 0.01$.

| | Low intensity light (LD 12:12) | | Darkness (DD) |
|---|---|---|---|
| Stage 1 larvae ($N$) | 5000 | | 2000 |
| Survival (%) | 54.3±12.95 | ** | 28.9±3.65 |
| Mean dry weight (mg) at stage IV | 6.3±0.40 | ** | 10.8±0.45 |
| Days to stage IV | 14.0±0.58 | | <14.0 |

Most larvae in these experiments molted to fourth stage during the dark phase. The possibility that this was related to the time that food was first given was eliminated by stocking and feeding larvae in both the light and dark phases of the LD 12:12 photoperiod. In the two treatments, survival was higher but development was slower when larvae were fed during the dark. However, the most significant result from this study was that the majority of larvae molt to fourth stage in the dark regardless of when the dark period occurs. Larvae reared and fed in a reversed photoperiod cycle molted in even greater numbers in the dark (Table 2), adjusting to a diurnal cycle 12 h out of phase with the photoperiod during embryonic development. It appears that larvae molt in response to timing of the scotophase rather than food availability.

Larvae were affected by the quality of brine shrimp used. The normal red-brown *Artemia* (Fig. 2, 3) produced the highest survival, greatest weight, and shortest development time. In contrast, fragmented brine shrimp produced the worst results (Table 3). The fragmented diet contained few intact shrimp and the small pieces may have reduced larval feeding success (see Anger and Nair 1979) or may have been lost rapidly through the drain screens. The pale brine shrimp did not affect survival but larvae weighed less at fourth stage, developed slower, were pale yellow, had a high incidence of missing chelipeds, and often had the cast shell still attached, suggesting a sublethal nutritional deficiency. Larvae on the pale diet molted almost as frequently in the light phase as in the dark phase (Table 3). These results cannot be ascribed solely to carotenoid content, since this stock of brine shrimp may have been generally deficient in nutrient value or contaminated in some way. However, these results support the principle that decreasing food availability or poor nutritional quality increases development time and decreases survival and growth in decapod larvae (Anger et al. 1985; Anger and Nair 1979; Carlberg and Van Olst 1976; Templeman 1936).

The larvae reared in continuous darkness were much heavier at fourth stage (10.8 mg) than those reared in LD 12:12 (5.5 mg) and were far heavier than larvae in any previous study

(Table 5). The rate of development in continuous darkness could not be determined, although it was faster than in LD 12:12. However, continuous darkness did reduce survival, a response also obtained with crab larvae (Dawirs 1982). An inverse relationship has been found between survival and weight in decapod larvae and has been attributed to cannibalism (see Anger and Nair 1979). However, the larvae reared in continuous darkness were so large that it appears that darkness affected size increase at molt. These differences in results between larvae reared in the dark and those reared under low light intensity indicate that lobster larvae perceive low light intensities.

When larvae were exposed to LD 12:12 at two light intensities, one 30 times greater than the other but still less than full sunlight, survival was higher in low light intensity. However, development rate was not affected. In March, larval weight was not affected by light intensity, but in May and July, larvae were heavier when reared under low light intensity.

In summary, our results extend previous observations that many environmental factors affect development of larvae (Aiken et al. 1981, 1982; Eagles et al. 1984). The need for a standardized diet for experiments on larvae is obvious, as frozen brine shrimp from a single commercial supplier produced dramatically different results. We have also demonstrated the requirement for a suitable feeding schedule, as the amount of food available during specific stages affects survival and development rate. Very large stage IV lobsters can be obtained by rearing larvae in continuous darkness, but larvae will survive better if reared in more normal daylengths under low light intensity.

## References


AIKEN, D. E., D. J. MARTIN, J. D. MEISNER, AND J. B. SOCHASKY. 1981. Influence of photoperiod on survival and growth of larval American lobsters (*Homarus americanus*). J. World Maricult. Soc. 12: 225–230.

AIKEN, D. E., W. J. ROWE, D. J. MARTIN-ROBICHAUD, AND S. L. WADDY. 1982. Seasonal differences in the effect of photoperiod on survival and development of larval American lobsters (*Homarus americanus*). J. World Maricult. Soc. 13: 287–293.

AIKEN, D. E., AND S. L. WADDY. 1985. Production of seed stock for lobster culture. Aquaculture 44: 103–114.

ANGER, K., AND K. K. C. NAIR.1979. Laboratory experiments on the larval development of *Hyas araneus*. Helgol. Wiss. Meersunters. 32: 36–54.

ANGER, K., V. STORCH, V. ANGER, AND J. M. CAPUZZO. 1985. Effects of starvation on molt cycle and hepatopancreas of stage I lobster (*Homarus americanus*) larvae. Helgol. Meeresunters. 39: 107–116.

BROWNLEE, K. A. 1960. Statistical theory and methodology in science and engineering. John Wiley & Sons Inc., New York, NY. 570 p.

CARLBERG, J. M., AND J. C. VAN OLST. 1976. Brine shrimp (*Artemia salina*) consumption by the larval stages of the American lobster (*Homarus americanus*) in relation to food density and water temperature. Proc. World Maricult. Soc. 7: 379–389.

D'ABRAMO, L. R., N. A. BAUM, C. E. BORDNER, AND D. E. CONKLIN. 1983. Carotenoids as a source of pigmentation in juvenile lobsters fed a purified diet. Can. J. Fish. Aquat. Sci. 40: 699–704.

DAWIRS, R. R. 1982. Methodical aspects of rearing decapod larvae, *Pagurus bernhardus* (Paguridae) and *Carcinus maenas* (Portunidae). Helgol. Meersunters. 35: 439–464.

EAGLES, M. D., D. E. AIKEN, AND S. L. WADDY. 1984. Effect of food quality and feeding schedule on survival, growth and development of larval American lobsters fed frozen adult brine shrimp. J. World Maricult. Soc. 15: 142–143.

FINNEY, D. J. 1952. Probit analysis. Cambridge University Press, New York, NY. 318 p.

FORD, R. F., R. R. FELIX, R. L. JOHNSON, J. M. CARLBERG, AND J. C. VAN OLST. 1979. Effects of fluctuation and constant temperatures and chemicals in thermal effluents on growth and survival of the American lobster (*Homarus americanus*). Proc. World Maricult. Soc. 10: 139–158.

HADLEY, P. B. 1906. Observations on some influences of light upon the larval and early adolescent stages of *Homarus americanus*: preliminary report. R.I. Comm. Inland Fish. Annu. Rep. 36: 237–257.

HARDING, G. C., K. F. DRINKWATER, AND W. P. VASS. 1983. Factors influencing the size of American lobster (*Homarus americanus*) stocks along the Atlantic coast of Nova Scotia, Gulf of St. Lawrence, and Gulf of Maine: a new synthesis. Can. J. Fish. Aquat. Sci. 40: 168–184.

HUNTSMAN, A. G. 1924. Limiting factors for marine animals. I. The lethal effect of sunlight. Contrib. Can. Biol. (N.S.) 2: 83–88.

KRINSKY, N. I. 1965. The carotenoids of the brine shrimp, *Artemia salina*. Comp. Biochem. Physiol. 16: 181–187.

PHILLIPS, B. F., AND A. N. SASTRY. 1980. Larval ecology, p. 11–57. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

SASAKI, G. C., J. M. CAPUZZO, AND P. BIESIOT. 1986. Nutritional and bio-energetic considerations in the development of the American lobster *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2311–2319.

STEEL, R. G. D., AND J. H. TORRIE. 1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw Hill Co., New York, NY. 481 p.

TEMPLEMAN, W. 1936. The influence of temperature, salinity light and food conditions on the survival and growth of the larvae of the lobster (*Homarus americanus*). J. Biol. Board Can. 2: 485–497.

# Nutritional and Bioenergetic Considerations in the Development of the American Lobster *Homarus americanus*[1]

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Sasaki, G. C., J. M. Capuzzo, and P. Biesiot. 1986. Nutritional and bioenergetic considerations in the development of the American lobster *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2311–2319.

To better understand the early life history stages of the American lobster *Homarus americanus*, nutritional and bioenergetic aspects of development have been investigated. These studies focused on physiological and biochemical processes during transitional periods between extrusion of the eggs, hatching, larval development, molting, metamorphosis, and attainment of the juvenile stage. Biochemical changes during embryogenesis reflect catabolism of various substrates for energy. Exposure to different thermal regimes resulted in considerable variation in the rates of utilization of energy substrates during embryogenesis. Embryos raised at elevated temperatures had yolk remaining at the time of hatching. The first three larval stages have similar energy requirements. Lipid is of prime importance and the turnover rate for lipid can be rapid. Weight-specific metabolism increases with successive larval stages. In stage IV lobsters, the dependency on lipid as a substrate is diminished and lipid reserves serve a storage function. Metabolic rates of premolt stage IV lobsters are decreased in comparison with earlier stages. These changes in physiology correlate with changes in the developing midgut gland, specifically with the appearance of droplets of lipid in the lipid-storing cells of the midgut gland of stage IV lobsters. By stage VI, lobsters have energy storage and metabolic patterns similar to those of adults, and the midgut gland has the adult morphology. The transitions from hatching to attainment of the juvenile form are reflected in differences in physiological and biochemical processes that influence food selection and diet.

Pour mieux comprendre les premiers stades du cycle vital du homard américain (*Homarus americanus*), les aspects alimentaire et bioénergétique du développement ont été examinés. Ces études ont été axées sur les processus physiologiques et biochimiques au cours des périodes de transition entre la sortie des oeufs, l'éclosion, le développement larvaire, la mue, la métamorphose et l'atteinte du stade juvénile. Les changements biochimiques au cours de l'embryogenèse reflètent le catabolisme de divers substrats au point de vue énergétique. L'exposition à différents régimes thermiques a amené une variation considérable des taux d'utilisation de substrats énergétiques pendant l'embryogenèse. Les embryons élevés à des températures élevées avaient encore du vitellus au moment de l'éclosion. Les trois premiers stades larvaires avaient des exigences énergétiques semblables. Les lipides sont d'une importance primordiale et le taux de roulement des lipides peut être rapide. Le métabolisme qui est fonction du poids augmente avec les stades larvaires successifs. Chez les homards du stade IV, la dépendance à l'égard des lipides en tant que substrat diminue et les réserves lipidiques ont une fonction d'entreposage. Les taux métaboliques des homards du stade IV avant la mue sont réduits par rapport aux stades antérieurs. Ces changements physiologiques présentent une corrélation avec les changements de la glande de l'intestin moyen en développement, particulièrement avec l'apparition de gouttelettes de lipides dans les lipocytes de la glande de l'intestin moyen des homards du stade IV. Au stade VI, les homards ont des régimes métaboliques et d'entreposage d'énergie semblables à ceux des adultes et la glande de l'intestin moyen a la morphologie de l'adulte. Les transitions entre l'éclosion et l'atteinte de la forme juvénile se reflètent par des différences dans les processus physiologiques et biochimiques qui influent sur le choix de la nourriture et sur le régime alimentaire.

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Development and metamorphosis of planktotrophic larvae, including those of decapod crustaceans, require efficient and coordinated utilization of available metabolic resources. Of many factors affecting resource utilization during the development period, nutrition is of prime importance. Nutrition involves endogenous and exogenous dietary sources, and the yolk reserve can be important during early postembryonic development. Consequently the nutritional aspects of embryogenesis are important for a complete understanding of development.

In the life cycle of the American lobster *Homarus americanus* Milne Edwards, there are several transitional periods where nutrition and bioenergetic processes may influence development. Embryogenic development of the lobster was described first by Bumpus (1891) and extends for 9–11 mo, depending on temperature (Templeman 1940; Perkins 1972; Branford 1978). During the embryogenic period, catabolism of yolk reserves serves as the sole source of nutrients for the developing embryo. At hatching and initiation of feeding, there

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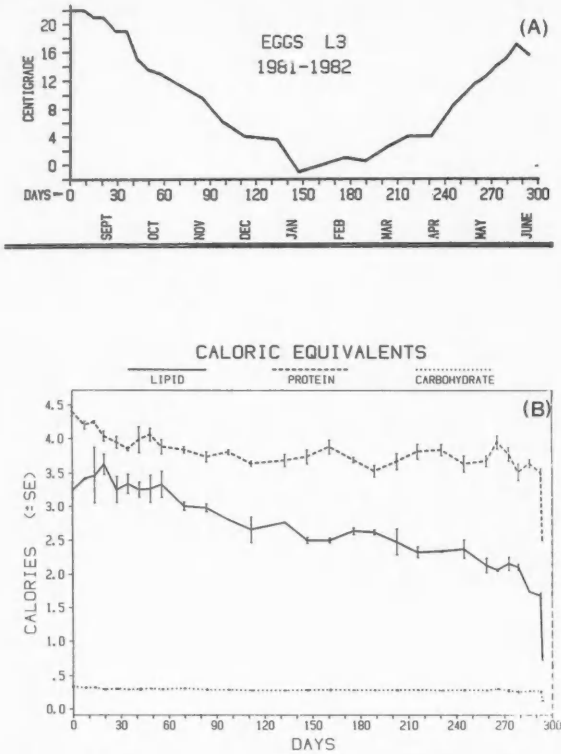


FIG. 1. (A) Temperature profile during embryogenesis study. (B) Caloric equivalents of protein, lipid, and carbohydrate during embryogenesis; values are presented as calories per individual ± SE; last point represents hatched larvae.

is a shift in dependence from endogenous to exogenous energy resources. Early development in the lobster includes four planktonic stages (Herrick 1896), although there is considerable debate whether or not these are all larval stages (Williamson 1982; Charmentier et al. 1984), as metamorphosis occurs at the molt between stages III and IV, but settlement does not take place until stage V. During development of the first three stages, there are gradual changes in morphology and concomitant changes in swimming behavior. After attainment of the fourth stage, claws are developed and more pronounced behavioral changes are evident. Stage IV lobsters are active swimmers but may remain among the plankton for several days before seeking a benthic habitat (Cobb 1976; Hughes and Matthiessen 1962). With the molt to stage V the shift to benthic habits is complete and feeding behavior is altered. With these changes, changes in metabolism, energy utilization, and biochemical composition may be expected and if so, may provide clues to changes in feeding requirements of young lobsters.

Capuzzo and Lancaster (1979) reported that weight-specific metabolism (oxygen consumption and ammonia excretion) of larvae of *H. americanus* increased with each stage (I–IV) and decreased with stage V. The rate of change in metabolism was greater than the rate of change in body size, indicating increased energy demand in the later larval stages. Reductions in O:N ratios among stages IV and V revealed an increased dependence on protein catabolism for energy. This paper presents an analysis of the physiological, biochemical, and morphological aspects of energy storage and metabolism in the early life history of *H. americanus*. Further elucidation of stage-specific changes in nutrition and bioenergetics is needed before the energetic costs of development are fully understood.

## Materials and Methods

### Culture Methods

*Embryogenic period*

To study the embryology of the lobster, gravid female lobsters were obtained prior to extrusion of their eggs. This was accomplished by examining the cement glands of the pleopods of female lobsters collected in local waters (Vineyard Sound, MA, and Buzzards Bay, MA). Cement gland morphology was examined according to the method described by Aiken and Waddy (1982). Lobsters that appeared ready to extrude eggs were placed individually in 95-L aquaria supplied with seawater (30–31‰ salinity) at ambient temperature (−0.5–22°C). The lobsters were fed frozen squid, clams, and fish twice a week. After extrusion, eggs were sampled from one female at weekly intervals at temperatures >6°C or biweekly intervals at temperatures <6°C until hatching occurred (295 d).

To examine the hatching period, eggs were sampled from lobsters that had extruded eggs before capture (offshore Buzzards Bay, MA). These lobsters were transferred to a 95-L aquarium supplied with flowing heated seawater (22–24°C) to accelerate embryogenesis. Hatching began after 120 d. Sampling of eggs began at the initiation of hatching and five samples were taken: (1) eggs 7–3 d from hatch, gold in color; (2) eggs 3 d to 12 h from hatch, gold; (3) eggs 1 d to hatching, blue; (4) prelarvae, or just prior to the molt to stage I; and (5) larvae within 6–36 h after hatching. The time until hatch for each sample was estimated and adjusted according to the time of the hatch.

Samples were assayed for biochemical composition according to the procedures described below. The morphology of the midgut gland in embryos and prelarvae were examined.

*Larval development*

Egg-bearing lobsters were obtained from offshore Buzzards Bay by fishermen and were transferred to individual 95-L aquaria, supplied with flowing seawater at ambient temperature and salinity (12–19°C; 30–31‰). Adult lobsters were fed frozen squid, clams, and fish twice weekly until hatching occurred. Hatching occurred over a 1- to 2-wk period, with the majority of larvae being released during 2–4 d. To provide animals as identical as possible, only larvae from one hatch, collected within 30 min of release, were used for each experiment. Each batch of larvae was placed in a separate fiberglass plankton-kriesel (Hughes et al. 1974), supplied with flowing, filtered (100 μm) seawater at ambient temperature (18–22°C); larvae were fed frozen *Artemia* (San Francisco Bay Brand) with a fatty acid supplement prepared from freeze-dried cod liver oil (Sasaki 1984) three to four times daily ad libitum). Larvae were sampled periodically and each larva was molt-staged according to the procedure of Sasaki (1984). Larvae were examined for changes in physiology, biochemical composition, and development of the midgut gland according to procedures described below.

### Physiological Measurements

Respiration rate of individual lobsters was measured at 20–

TABLE 1. Weight and eye dimensions of embryos of *Homarus americanus* ($n$ = 10).

| Date 1981–82 | Wet weight (mg) ±1 SD | Dry weight (mg) ±1 SD | Egg diameter (range in mm) | Eye length (range in mm) | Eye width (range in mm) |
|---|---|---|---|---|---|
| Aug. 24 | 2.10±0.11 | 1.03±0.05 | 1.4–1.6 | | |
| Sept. 1 | 2.08±0.05 | 1.01±0.04 | 1.4–1.5 | | |
| Sept. 7 | 2.17±0.06 | 1.07±0.03 | 1.4–1.6 | | |
| Sept. 13 | 2.15±0.09 | 1.01±0.04 | 1.5–1.6 | | |
| Sept. 21 | 2.20±0.08 | 1.03±0.05 | 1.5–1.6 | 0.09–0.11 | |
| Sept. 28 | 2.31±0.08 | 1.02±0.02 | 1.5–1.6 | 0.15–0.16 | |
| Oct. 5 | 2.39±0.08 | 1.03±0.05 | | 0.22–0.24 | 0.13–0.15 |
| Oct. 12 | 2.37±0.04 | 1.02±0.02 | 1.5–1.6 | 0.25–0.27 | 0.16–0.18 |
| Oct. 19 | 2.48±0.08 | 1.04±0.04 | 1.5–1.7 | 0.26–0.33 | 0.19–0.21 |
| Nov. 2 | 2.63±0.09 | 1.04±0.03 | 1.6–1.8 | 0.36–0.40 | 0.24–0.28 |
| Nov. 16 | 2.63±0.09 | 0.99±0.05 | 1.7–1.8 | 0.43–0.50 | 0.30–0.33 |
| Nov. 30 | 2.67±0.07 | 1.00±0.04 | 1.7–1.8 | 0.43–0.46 | 0.30–0.31 |
| Dec. 14 | 2.71±0.06 | 1.01±0.03 | 1.7–1.8 | 0.43–0.46 | 0.30–0.32 |
| Jan. 4 | 2.60±0.03 | 0.97±0.02 | 1.7–1.8 | 0.40–0.46 | 0.26–0.30 |
| Jan. 18 | 2.62±0.12 | 0.97±0.06 | 1.7–1.8 | 0.41–0.48 | 0.26–0.30 |
| Feb. 1 | 2.54±0.09 | 0.94±0.04 | 1.7–1.8 | 0.43–0.46 | 0.26–0.30 |
| Feb. 16 | 2.61±0.06 | 0.98±0.03 | 1.7–1.8 | 0.42–0.46 | 0.30–0.35 |
| Mar. 1 | 2.61±0.02 | 0.96±0.03 | 1.7–1.8 | 0.43–0.47 | 0.26–0.30 |
| Mar. 15 | 2.58±0.10 | 0.96±0.04 | 1.7–1.8 | 0.44–0.47 | 0.30–0.33 |
| Mar. 28 | 2.62±0.05 | 0.98±0.03 | 1.7–1.8 | 0.43–0.47 | 0.30–0.34 |
| Apr. 12 | 2.61±0.08 | 0.95±0.03 | 1.7–1.8 | 0.43–0.47 | 0.30–0.34 |
| Apr. 26 | 2.57±0.10 | 0.92±0.05 | 1.7–1.8 | 0.40–0.46 | 0.30–0.33 |
| May 10 | 2.64±0.08 | 0.92±0.05 | 1.7–1.8 | 0.43–0.46 | 0.30–0.33 |
| May 17 | 2.62±0.07 | 0.92±0.04 | 1.7–1.9 | 0.44–0.46 | 0.30–0.36 |
| May 24 | 2.60±0.13 | 0.93±0.05 | 1.7–1.8 | 0.44–0.48 | 0.30–0.33 |
| May 30 | 2.74±0.10 | 0.88±0.05 | 1.7–2.0 | 0.46–0.53 | 0.30–0.33 |
| June 6 | 3.18±0.13 | 0.92±0.03 | 1.7–2.0 | 0.50–0.56 | 0.33–0.39 |
| June 13 | 3.32±0.22 | 0.91±0.03 | 1.8–2.1 | 0.49–0.59 | 0.36–0.40 |

TABLE 2. Losses in lipid classes associated with hatching ($n$ = 3).

| Sample | Total lipid | Triacylglycerol (mean μg·individual$^{-1}$ ± SD) | Phosphatidyl choline (mean μg·individual$^{-1}$ ± SD) |
|---|---|---|---|
| Gold egg A | 287 | 121.2±8.0 | 99.7±7.0 |
| Gold egg B | 254 | 88.0±6.4 | 94.6±6.7 |
| Blue egg | 221 | 67.9±8.4 | 82.7±9.2 |
| Prelarva | 215 | 64.4±1.3 | 88.2±4.0 |
| St. 1 larva | 207 | 59.7±2.1 | 81.7±3.0 |

22°C after acclimation to 20°C using a microrespirometer and a Gilson differential respirometer according to techniques described by Capuzzo and Lancaster (1979). Equilibrium between the gas and liquid phase of $O_2$ diffusion in the respirometer flasks was enhanced by gently shaking the flasks. At the end of each set of oxygen uptake measurements, the seawater in the respirometer flasks was analyzed for $NH_4^+$-N by the method of Solorzano (1969) in order that an in situ O:N ratio (atomic ratio of oxygen consumed to $NH_4^+$-N excreted) could be made; ammonia levels were compared with control blanks.

## Biochemical Analyses

Eggs were detached from their surrounding cement matrix and measured with an ocular micrometer in a dissecting scope and the greatest egg diameter was recorded. If present, the embryonic eye width was measured (Perkins 1972). Eggs were then dipped into distilled water to remove external salt and blotted dry on a paper towel. Larvae were placed on a fiberglass mesh, dipped in distilled water, and blotted dry on a paper towel. Three samples of two eggs were pooled and taken for ash analysis, four samples of two eggs were pooled and taken for protein and carbohydrate analyses, and two samples of 10 eggs were pooled and taken for lipid analyses. For larval samples, three individuals were used for determination of ash values, four for protein and carbohydrate, and two groups of two to five individuals were pooled for lipid analyses. Each sample was measured for wet weight to the nearest 0.1 mg on a Mettler H15 balance. Samples for ash, protein, and carbohydrate analyses were frozen and lyophilized, weighed to the nearest 0.01 mg on a Mettler M5 microbalance, and stored at −20°C until analysed. Ash levels were determined after combustion at 475°C, carbohydrate levels were determined according to the procedure of Dubois et al. (1956), and protein levels were determined by the Lowry procedure (Hartree 1972) or using a Coomassie blue procedure (BioRad Laboratories 1979). For lipid analyses, egg and larval samples were weighed (wet weight) and extracted immediately for lipids (Folch et al. 1957; Sasaki and Capuzzo 1984). Total lipid was determined gravimetrically and lipid classes were determined using a Newman-Howells Iatroscan TH-10 according to the procedure described by Sasaki and Capuzzo (1984). A more detailed

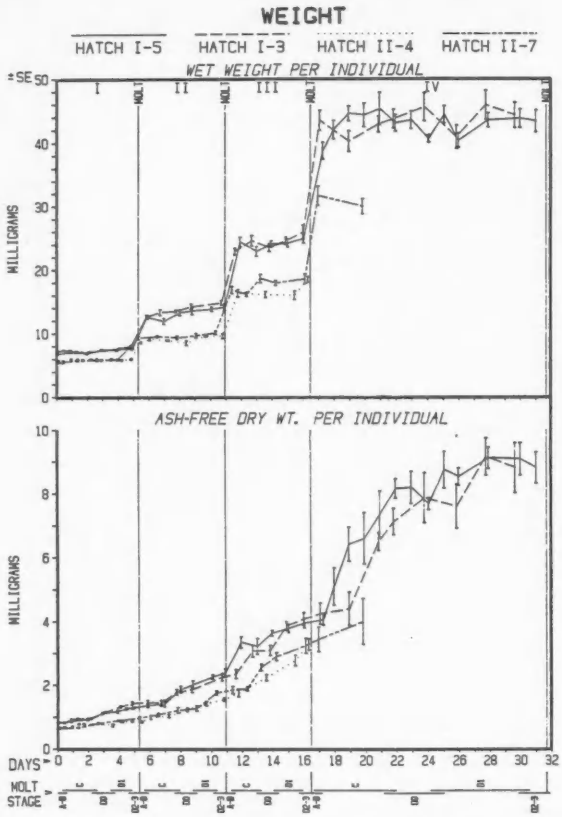


FIG. 2. Wet weight and ash-free dry weight of four hatches of lobsters; each value is the mean of seven measurements ± SE. The vertical lines labelled "MOLT" indicate the time of molting; the roman numerals (I–IV) at the top of the graph indicate each stage.

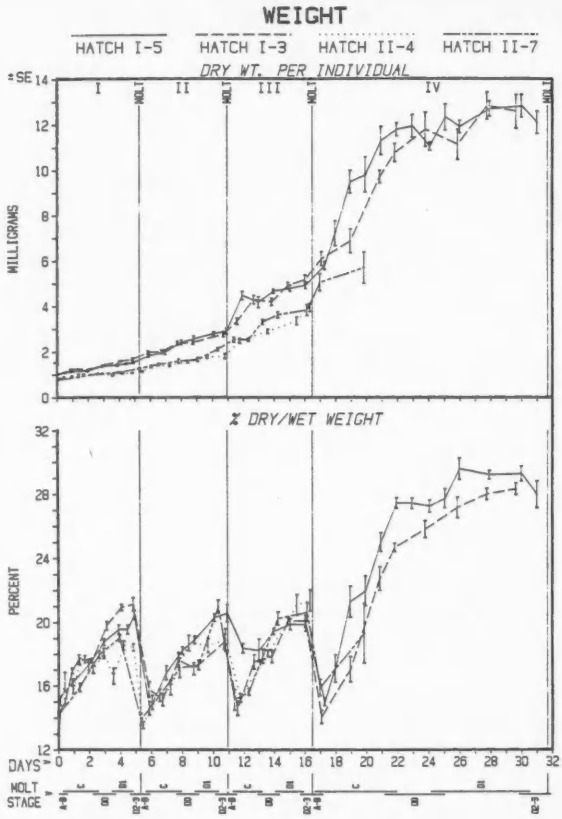


FIG. 3. Dry weight and percent dry to wet weight ratios of larval lobsters; each value is the mean of seven measurements ± SE.

description of analytical procedures is presented in Sasaki (1984).

### Histological Methods

Embryos used to examine the morphology of the developing midgut gland were removed from the egg mass of a lobster. Larval and juvenile lobsters were sampled from laboratory cultures; animals were molt-staged and only intermolt animals were used. Whole animals were fixed in 3% phosphate-buffered glutaraldehyde, pH 7.2, for 1.5–2 h at 7°C. The tissues were washed in cold 0.1 *M* phosphate buffer and run through a dehydration series from 50 to 95% ethanol. Plastic embedding medium (methacrylate) was used according to the manufacturer's instructions (Polyscience, Inc.). The tissues were sectioned at 2 μm on a Sorvall JB-4 microtome and mounted on clean glass microscope slides. The sections were stained with Lee's methylene blue-basic fuchsin. To demonstrate the presence of yolk in the midgut gland, newly hatched stage I larvae were held separately for 12 h until attainment of molt stage C before being sampled; the larvae were fixed in glutaraldehyde as described above. After fixation, the midgut glands were dissected out and washed in buffer. They were postfixed for 2 h on ice in 1% osmium tetroxide buffered with 0.1 *M* phosphate buffer plus 0.75 g sucrose $\cdot L^{-1}$ and washed in cold buffer. The tissues were dehydrated and embedded as described above.

### Statistical Methods

Differences in parameters among the various developmental stages were assessed by Student's *t*-test and analysis of variance (Sokal and Rohlf 1969; Zar 1974).

## Results

The temperature profile of the incubation period for the embryological study is presented in Fig. 1A. Egg diameter, weight, and eye width and length measurements of the developing embryo are presented in Table 1. The wet weight of the egg increased for 10 wk and remained constant until approximately 3 wk prior to hatching when a second increase occurred. Wet weight increase, due to water absorption, was reflected in an increase in egg size. There was a decline in dry weight throughout embryogenesis. Loss of both wet weight and dry weight occurred at hatching and produced a large drop in the dry to wet weight ratio. The greatest change in biochemical composition was observed during the month after fertilization and in the month prior to hatching. Protein, lipid, and carbohydrate levels, expressed as their caloric equivalents, are

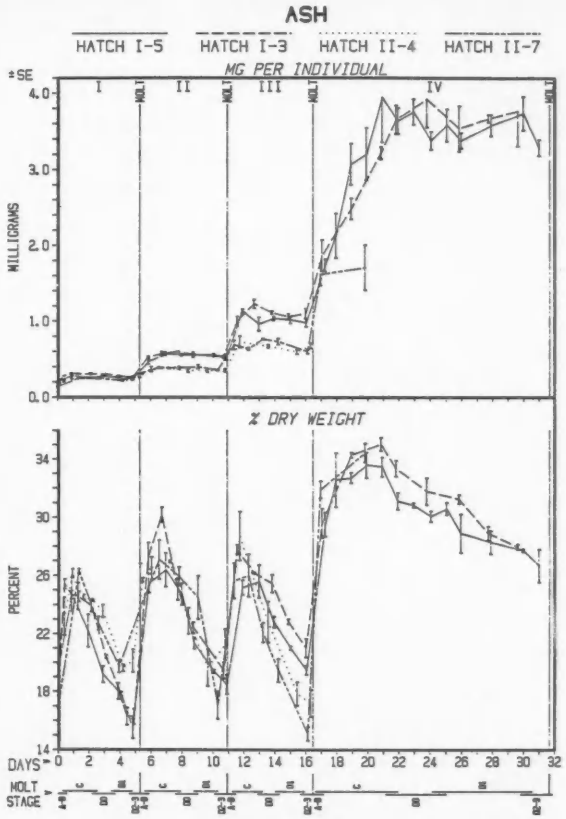


FIG. 4. Ash levels of larval lobsters; each value is the mean of three measurements ± SE.

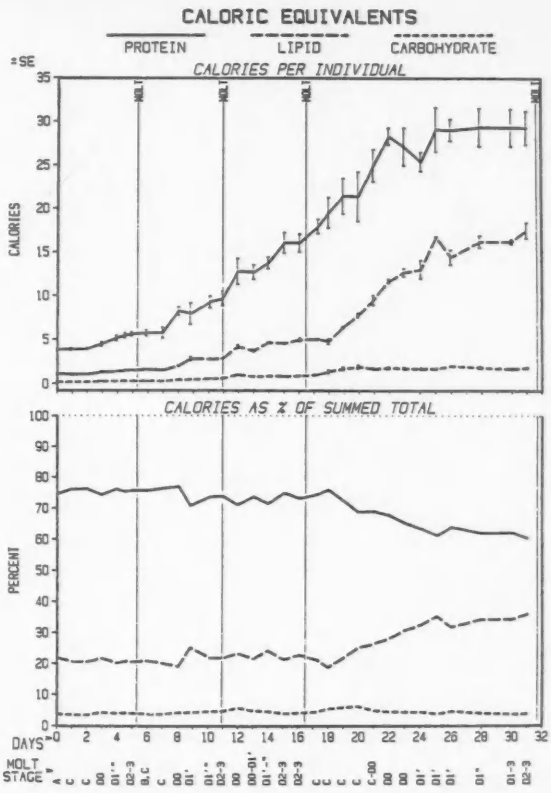


FIG. 5. Caloric equivalents for protein, lipid, and carbohydrate levels of larval lobsters; each value is the mean of four measurements for protein and carbohydrate and two measurements for lipid ± SE.

presented in Fig. 1B. Little or no change in carbohydrate level occurred, whereas protein levels decreased gradually during the initial phases of embryogenesis and then stabilized until hatching. Lipid levels decreased throughout the embryonic period and the loss was accentuated at hatch. The change during embryogenesis was greatest for lipids, followed by protein and carbohydrate. Using heat of combustion factors (Kleiber 1975) for protein (5.7 cal·mg$^{-1}$), carbohydrate (4.0 cal·mg$^{-1}$), and lipid (9.5 cal·mg$^{-1}$), it was determined that protein declined by 0.90 cal·egg$^{-1}$ and lipid declined by 1.57 cal·egg$^{-1}$ during embryogenesis (fertilization to the last egg sample). Losses of protein, carbohydrate, and lipid were used to estimate the caloric cost of embryogenesis; a value of 2.53 cal was estimated, indicating a yolk utilization efficiency of 68.4%. If the increased energetic costs of hatching are included in this estimate (including the caloric loss of the egg membrane = 0.33 cal; Pandian 1970), then yolk utilization efficiency was 46.7%. The decreases of triacylglycerol, phosphatidyl choline, and phosphatidyl ethanolamine throughout embryogenesis accounted for 74, 23, and 9%, respectively, of the total lipid loss.

Differences in biochemical composition of larvae at hatch were observed between samples from the embryogenesis study and the hatching period study, with larvae from the latter study having relatively larger energy reserves at hatch. It is speculated that this extra energy represents the energy not required for maintenance during periods of low temperatures. The main difference was in the amount of lipid remaining at hatch (0.12 mg·individual$^{-1}$; 1.14 cal·individual$^{-1}$). Eggs sampled during the embryogenesis study showed a decline of 0.05 mg of lipid during the period when the temperature was <6°C. The difference in these lipid values provides an approximation of the metabolic cost of maintenance under the temperature regimes experienced under ambient conditions and indicates a possible increased efficiency of development at higher temperatures. This excess lipid can serve as a supplemental energy store during the early posthatch period (Sasaki 1984). Changes in lipid composition (total, triacylglycerols, and phosphatidyl choline) at hatching are presented in Table 2.

The wet weight of larvae increased at each molt (Fig. 2). After this increase, the weight remained relatively stable until the next molt. The increase in wet weight at molt ranged from 70 to 80%. Dry weight (Fig. 3) and ash-free dry weight (Fig. 2) increased gradually and were not affected strongly by the molt. When the dry weight data are presented as a percentage of wet weight, a consistent relationship is seen for the first three larval stages. In stage IV lobsters, the dry weight increased to 28% of the wet weight.

Ash level increased after each molt and reached maxima during intermolt in each stage (Fig. 4); as a percentage of dry weight values, ash declined after intermolt in each stage. In stage IV lobsters, ash comprised a relatively greater proportion

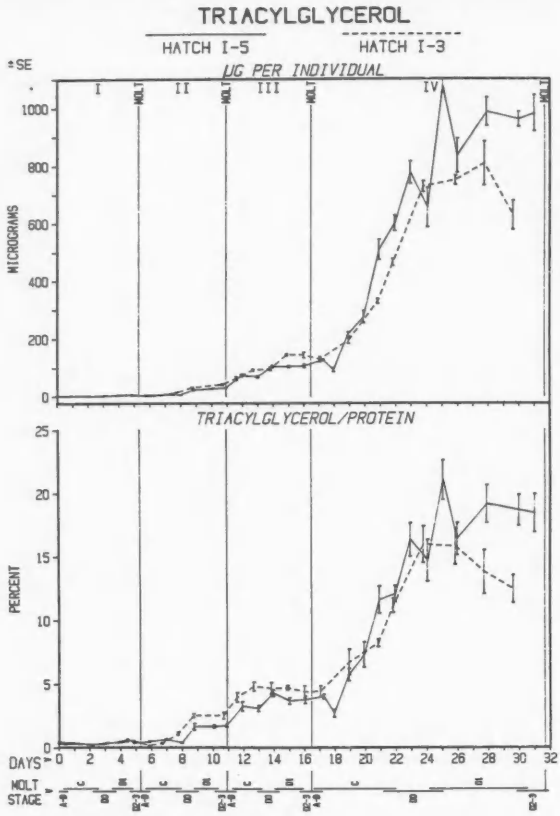


FIG. 6. Triacylglycerol levels and triacylglycerol to protein ratios of larval lobsters; each value is the mean of three measurements ± SE.

of total weight than in stages I–III.

Protein, lipid, and carbohydrate levels, reported as caloric equivalents, are presented in Fig. 5. Protein was the largest biochemical constituent in all stages; as a percentage of all biochemical components, however, protein decreased in stage IV lobsters as lipid levels increased. Carbohydrate remained at a low but stable level throughout larval development. Triacylglycerol levels did not increase until the middle of the second larval stage (Fig. 6). Accumulation of triacylglycerol then occurred at a steady rate until stage IV-C when it increased rapidly until stage IV-$D_1$, when it began to stabilize. As a percent of total lipid content, triacylglycerol increased from <3% at hatch to >50% in stage IV-$D_1$ lobsters and was the major lipid component. Triacylglycerol to protein ratios increased throughout development, indicating no constant relationship between the two parameters.

Respiration rates of larval lobsters (stages I–III) increased slightly during the molt cycle (molt stage B-$D_1$) following a slight decline during the postmolt recovery period (A–B). Increases in respiration rate were evident with the molt to subsequent stages with the exception of the molt to stage V (Fig. 7). Weight-specific respiration rates increased with each molt stage and were highest among stage IV larvae, and then decreased just prior to the molt to stage V ($D_3$). Ammonia excretion rates followed similar patterns as respiration rates in stages I and II, increased with stage III and stage IV, and

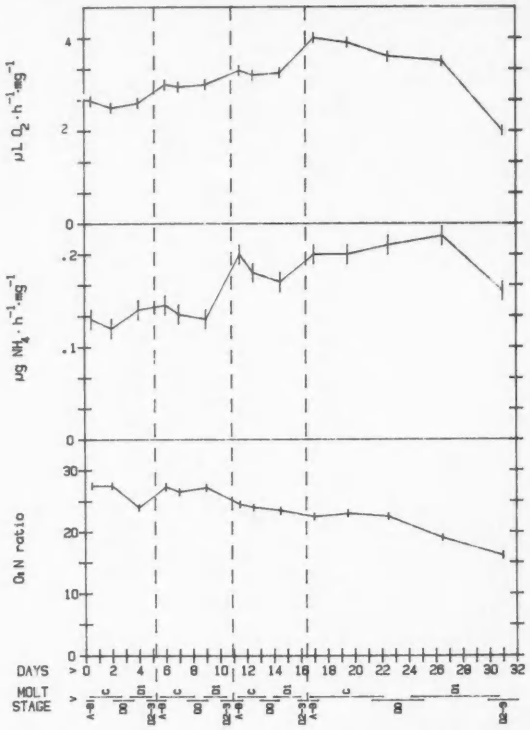


FIG. 7. Respiration rates, ammonia excretion rates, and O:N ratios of larval lobsters; each value is the mean of 24 measurements ± SE.

decreased just prior to the molt to stage V; in stages I, II, and III, ammonia excretion rates increased immediately after molting. O:N ratios were similar for stages I and II, decreased slightly for stage III, and showed a steady decline among stage IV lobsters, with the lowest value recorded just prior to the molt to stage V. The level of significance for differences in metabolic rates among each larval stage was $P < 0.01$.

The R-cells of the midgut gland, which function in adult crustaceans to store lipids, serve a similar purpose during early development of the American lobster. Late embryos, prelarvae, and unfed stage I larvae have lipid droplets, derived from the yolk, stored in R-cells (Fig. 8). Larval stages (stages I, II, and III) show no sign of lipid storage in the midgut gland (Fig. 9). Stage IV lobsters begin to store lipids, as evidenced by the appearance of a few lipid droplets in the R-cells. By stage VI, there are extensive lipid stores in the digestive gland. The morphology of the lipid-storing cells in juvenile lobsters is indistinguishable from that of adult lobsters, although the tubule formation in the midgut gland is less extensive. A more detailed description of the morphology of the midgut gland is reported by Biesiot (1986).

## Discussion

The most active periods during embryogenesis, in terms of rates of utilization of biochemical constitutents, were the month after fertilization and the month prior to hatching. Utilization of lipid and protein reserves during embryogenesis had different patterns; loss of protein and lipid did not occur at the

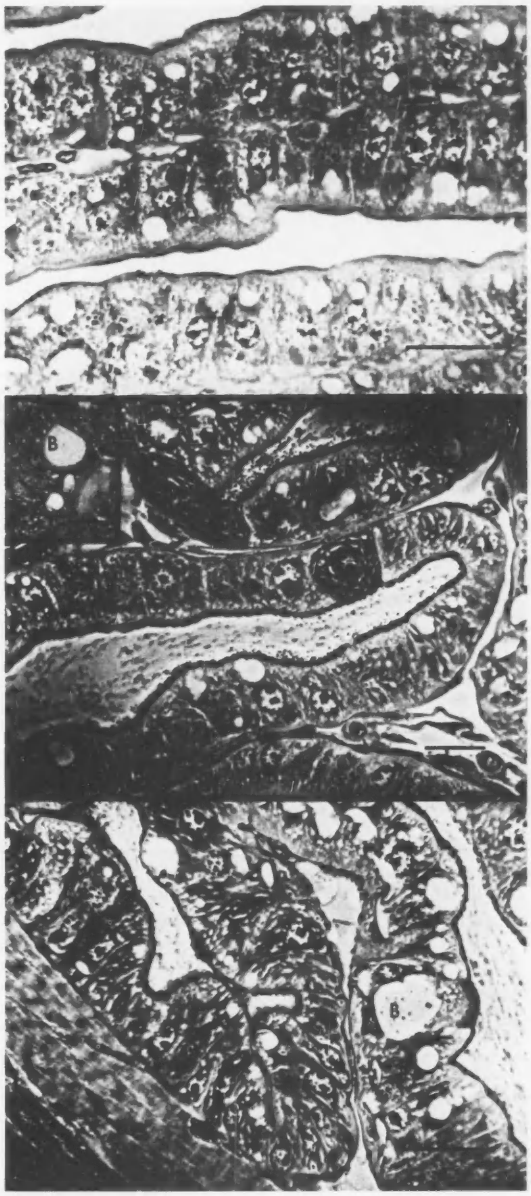


FIG. 8. Cell types comprising the midgut gland in embryonic stages: (A) gold egg, 3 d prior to hatch, scale bar = 5 μm; (B) blue egg, early in hatching process, scale bar = 5 μm; inset, B-cell, scale bar = 2 μm; (C) prelarva, late in hatching process. R = R-cell, F = F-cell, B = B-cell, a = apical complex of B-cell.

same rate throughout embryogenesis. Lipid provided the major portion of metabolic energy during embryogenesis, consistent with observations on other crustaceans (Barnes 1965; Pandian 1967, 1970; Pandian and Schumann 1967). If lipid reserves were sufficient to provide all the energy necessary for embryogenesis, then the loss of protein (~20%) during this period may be due to inefficient conversion from yolk protein to tissue and not due to respiratory needs. A latent period during mid-embryogenesis was observed when no change in protein level was evident. In contrast, lipid showed a steady decline throughout embryogenesis. Most of the lipid catabolized was triacylglycerol, but phosphatidyl choline was also used to some extent and may provide a secondary energy source when triacylglycerol is depleted. Increased conversion efficiency of embryos incubated at elevated temperatures suggests that subtle variations in the energetics of embryogenesis may be apparent among different populations where thermal regimes are different (Cooper and Uzmann 1980). Yolk in posthatch larvae may delay feeding and prolong periods of starvation resistance (Sasaki 1984; Anger et al. 1985) and would be of considerable adaptive advantage to newly hatched larvae.

The biochemical composition of lobster larvae reveals several clues as to the comparative aspects of bioenergetics during larval development and metamorphosis. Upon ecdysis, larvae absorbed water, increased in size, and began formation of the new exoskeleton. Decreases in carbohydrate and protein were likely related to chitin formation and, with decreases in lipid, energy utilization. Higher O:N ratios and a lack of evidence of lipid storage in the early larval stages suggest a reliance on catabolism of mixed energy substrates. Stage IV and V animals showed an increased dependence on protein catabolism. Carbohydrate, protein, and lipid increased from intermolt to early premolt stages, either through synthesis of new tissue and/or accumulation of energy reserves. Although respiration rates, ammonia excretion rates, and O:N ratios were fairly consistent within the molt cycle of an individual larval stage, significant increases in ammonia excretion rates, evident in the early postmolt periods, may reflect protein-fueled gluconeogenesis to produce chitin for the exoskeleton. The increased ash content of stage IV lobsters is indicative of the development of a more heavily calcified exoskeleton in postmetamorphic animals.

Accumulation of energy reserves may be related to life style, whereby active, rapidly growing animals with quick molt recoveries (stages I, II, and III) store less reserves than larger, slower growing animals (juveniles and adults) with more prolonged molt recovery periods. Thus, the transitions observed between stage I and stage IV lobsters may reflect comparative energetic strategies for different habitats. Postmetamorphic animals accumulated greater proportions of lipid, as evidenced by both biochemical studies and histological studies of the midgut gland. The reasons for this accumulation are unknown. On a caloric basis, the increased triacylglycerol content of late stage IV lobsters accounts for 3–5 d of metabolic reserves, based on measurements of routine oxygen consumption. As new feeding behavior must be adopted in benthic habitats, newly settled lobsters may rely temporarily on stored reserves. Premetamorphic larvae show little evidence of lipid storage and appear to utilize lipid rapidly. The lipid storage patterns seen in stage IV lobsters were consistent with the findings of increased protein catabolism (lower O:N ratios) and a reduction in metabolic activity of late premolt animals.

The physiological and biochemical observations made in this study have several implications for assessing the early life history of lobster populations. The large changes seen in energy storage and utilization patterns between pre- and post-metamorphic animals suggest that lipid stores may have an advantage for newly settled lobsters in that sufficient reserves may be available for searching for a suitable substrate, burrow construction, and adapting to a new habitat before feeding is a

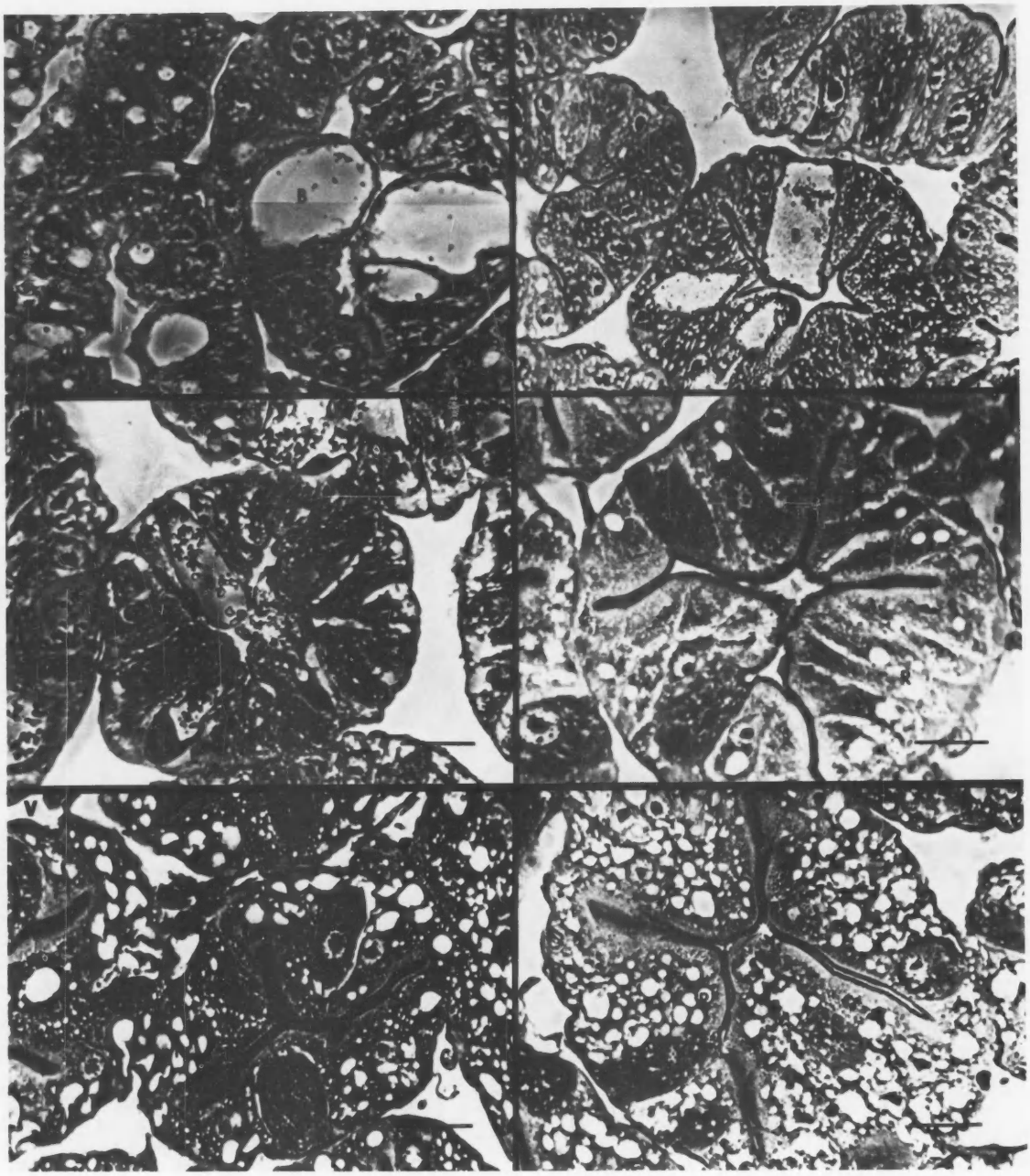


FIG. 9. Cell types comprising the midgut gland intermolt stages I–VI.

necessity. These studies also suggest that the transitional period between planktonic and benthic existence correlates with the capacity for increased energy stores and that larvae at molt stage IV-$D_0$–$D_1$ are at a considerable energetic advantage in selecting a benthic habitat. Settlement of larval lobsters may therefore be delayed until after this energetic transition.

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## References


AIKEN, D. E., AND S. L. WADDY. 1982. Cement gland development, ovary maturation and reproductive cycles in the American lobster, *Homarus americanus*. J. Crustacean Biol. 2: 315–327.

ANGER, K., V. STORCH, V. ANGER, AND J. M. CAPUZZO. 1985. Moult cycle and hepatopancreas of lobster larvae. Helgol. Meeresunters. 39: 107–116.

BARNES, H. 1965. Studies in the biochemistry of cirripede eggs. 1. Changes in the general biochemical composition during development of *Balanus balanoides* and *B. balanus*. J. Mar. Biol. Assoc. U.K. 45: 321–339.

BIESIOT, P. M. 1986. Changes in midgut gland morphology and digestive enzyme activities associated with development in early stages of the American lobster *Homarus americanus*. Ph.D. thesis, MIT-WHOI, WHOI-86-20.

BIORAD LABORATORIES. 1979. BioRad protein assay. Bulletin 1069, February 1979, Richmond, CA.

BRANFORD, J. R. 1978. Incubation period for lobster *Homarus americanus* at various temperatures. Mar. Biol. 47: 363–368.

BUMPUS, H. 1891. The embryology of the American lobster. J. Morphol. 5: 215–262.

CAPUZZO, J. M., AND B. A. LANCASTER. 1979. Some physiological and biochemical considerations of larval development in the American lobster, *Homarus americanus* Milne Edwards. J. Exp. Mar. Biol. Ecol. 40: 53–62.

CHARMENTIER, G., M. CHARMENTIER-DOURES, AND D. E. AIKEN. 1984. Neuroendocrine control of hydromineral regulation in the American lobster *Homarus americanus* H. Milne Edwards, 1837. Gen. Comp. Endocrinol. 54: 20–34.

COBB, J. S. 1976. The American lobster: the biology of *Homarus americanus*. Sea Grant Tech. Rep., University of Rhode Island, Kingston, RI.

COOPER, R. A., AND J. R. UZMANN. 1980. Ecology of juvenile and adult *Homarus*, p. 97–142. *In* J. S. Cobb and B. F. Philips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

DUBOIS, M., K. A. GILES, J. K. HAMILTON, P. A. REBERS, AND F. SMITH. 1956. Colorimetric method for determination of sugars and related substances. Anal. Chem. 28: 350–356.

FOLCH, J., N. LEES, AND C. H. SLOANE-STANLEY. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226: 497–509.

HARTREE, E. F. 1972. Determination of protein: a modification of the Lowry method that gives a linear photometric response. Anal. Biochem. 48: 422–427.

HERRICK, F. H. 1896. The American lobster: a study of its habits and development. Bull. U.S. Fish. Comm. 15: 1–252.

HUGHES, J. T., AND G. C. MATTHIESSEN. 1962. Observations on the biology of the American lobster *Homarus americanus*. Limnol. Oceanogr. 7: 414–421.

HUGHES, J. T., R. A. SCHLESER, AND G. TCHOBANOGLOUS. 1974. A rearing tank for lobster larvae and other aquatic species. Prog. Fish-Cult. 36: 129–132.

KLEIBER, M. 1975. The fire of life. Robert E. Krieger Publishing Co., Huntington, NY.

PANDIAN, T. J. 1967. Changes in chemical composition and caloric content of developing eggs of the shrimp, *Crangon crangon*. Helgol. Wiss. Meeresunters. 16: 216–224.

1970. Ecophysiological studies on the developing eggs and embryos of the European lobster, *Homarus gammarus*. Mar. Biol. 5: 154–176.

PANDIAN, T. J., AND K. H. SCHUMANN. 1967. Chemical composition and caloric content of egg and zoea of the hermit crab, *Eupagurus bernhardus*. Helgol. Wiss. Meeresunters. 16: 225–230.

PERKINS, H. C. 1972. Developmental rates at various temperatures of embryos of the northern lobster (*Homarus americanus* Milne Edwards). Fish. Bull. 70: 95–99.

SASAKI, G. C. 1984. Biochemical changes associated with embryonic and larval development in the American lobster *Homarus americanus* Milne Edwards. Ph.D thesis, MIT/WHOI, WHOI-84-8.

SASAKI, G. C., AND J. M. CAPUZZO. 1984. Degradation of *Artemia* lipids under storage. Comp. Biochem. Physiol. 78B: 525–531.

SOKAL, R. R., AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, CA.

SOLORZANO, L. 1969. Determination of ammonia in natural waters by the phenol–hypochlorite method. Limnol. Oceanogr. 14: 799–801.

TEMPLEMAN, W. 1940. Embryonic developmental rates and egg laying of Canadian lobsters. J. Fish. Res. Board Can. 5: 71–83.

WILLIAMSON, D. I. 1982. Larval morphology and diversity, p. 43–110. *In* L. G. Abele [ed.] The biology of Crustacea. Vol. 2. Embryology, morphology, and genetics. Academic Press, New York, NY.

ZAR, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, NJ.

# Evaluation of the Role of Nutrition in Lobster Recruitment

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Castell, J. D., and J. C. Kean. 1986. Evaluation of the role of nutrition in lobster recruitment. Can. J. Fish. Aquat. Sci. 43: 2320–2327.

Many of the hypotheses and proposals presented here on the role of nutrition in lobster recruitment have been derived from research on other aquatic animals. Little research has focused on the determination of nutritional requirements of lobsters and even that has been primarily with small juveniles (36–1000 mg). Despite the tacit acknowledgement that maternal fecundity and egg viability are a function of quantity and quality of available food, little is known about the nutrition of reproductively mature lobsters. The importance of broodstock nutrition and possible methods for evaluating nutritional status are discussed. Information on protein, essential amino acids, vitamins, minerals, carbohydrates, and lipids is summarized. Additionally, some proposals for field application of nutritional response criteria used in the laboratory are discussed. Though research on larvae, adult, broodstock nutrition, effects of environmental factors (e.g. temperature, salinity, photoperiod, etc.), as well as many other aspects of nutrition is yet to be done, there is "good opportunity" for nutrition to be a significant part of the current lobster recruitment research program.

Bon nombre des hypothèses et des propositions présentées ici sur le rôle de la nutrition dans le recrutement des homards ont été tirées de recherches portant sur d'autres animaux aquatiques. Rares sont les recherches qui portaient sur les besoins alimentaires des homards, et elles touchaient principalement les petits juvéniles (36–1 000 mg). S'il est tacitement reconnu que la fécondité maternelle et la viabilité des oeufs sont fonction de la quantité et de la qualité de la nourriture disponible, on sait peu de choses sur la nutrition des homards à la maturité sexuelle. Nous étudions l'importance de la nutrition des géniteurs et les méthodes pouvant permettre d'évaluer leur état sur le plan de la nutrition. Nous résumons l'information sur les protéines, les acides aminés essentiels, les vitamines, les minéraux, les hydrates de carbone et les lipides. Nous examinons de plus certaines propositions d'application sur le terrain des critères de réaction nutritionnelle employés en laboratoire. Bien qu'il reste beaucoup de recherches à faire sur la nutrition des larves, des adultes et des géniteurs, sur les effets des facteurs environnementaux (p. ex. la température, la salinité, la photopériode, etc.) ainsi que sur de nombreux autres aspects de la nutrition, il semble très opportun que la nutrition constitue une partie importante du programme actuel de recherche sur le recrutement des homards.

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The American lobster, *Homarus americanus*, is one of the most valuable single species in the Canadian fishing industry. The most efficient exploitation of this, as well as other commercially important species, will depend on an understanding of all the factors that affect existing and future catchable stocks. There is increasing evidence that both quantitative and qualitative nutritional factors play an important role in determining year class strength of exploited fishery stocks, including lobster.

The concept of the availability of food has been incorporated into many recruitment theories in the past. Hjort (1914) postulated that food deficiencies of first-feeding larvae may be primarily responsible for the observed variation in the abundance of recruits. This hypothesis was expanded to include the concept of a point-of-no-return, a critical starvation period, after which first-feeding larvae could not survive, even if food should become available (Blaxter and Hempel 1963, McGurk 1984, Anger et al. 1985). Lasker and Smith (1977) discussed a "coincidence theory" in which a patch of larvae will survive only if it coincides with an adequate patch of food organisms. Cushing (1973) indicated that a critical phase in a population may occur during the period of larval drift when density-dependent processes (e.g. competition for food) are at their maximum. A panel concluded that the major causes of larval mortality were starvation and predation, and that these may interact (Hunter 1976).

As the lobster grows from a pelagic 6-mg larva to a 1- to 10-kg benthic adult, both the size and the type of organisms consumed change. Seasonal, environmental, annual, and geographic variations will result in differences in the diet of lobsters even when they are the same size. In evaluating the nutritional significance of variations in food organisms it will be important to consider essential nutrients such as vitamins, trace elements, amino acids, fatty acids, and other lipids. Nonessential nutrients such as carbohydrates, saturated and monoenoic fatty acids, and dispensible amino acids are also important in considerations of nutritional value. Other nutritional factors such as protein/energy ratios, digestibilities, crude fiber, and water content and even antinutritional factors such as insecticides, toxic heavy metals, polychlorinated biphenols, vitamin and digestive enzyme inhibitors, etc., must not be overlooked when evaluating the nutritional impact of food organisms in recruitment models. Direct evidence for the effects of nutritional quality of food on lobster recruitment is

limited; however, there are sufficient examples for fish and other crustaceans to suggest that similar effects may exist.

This paper reviews the known nutritional limitations on reproduction and larval and juvenile growth and survival in several fish and crustacean species. From this evidence, procedures and experimental designs are suggested which will facilitate the assessment of both qualitative and quantitative nutritional effects on lobster well being and recruitment.

## Nutritional Relationships between Primary and Secondary Producers

Variations in the nutritional value of the predominant species that occur in sequential algal blooms may affect the survival of dependent fishes. Lasker (1981) reported that northern anchovy larvae, *Engraulis mordax*, underwent heavy mortalities when the dinoflagellate *Gonyaulax polyedra* was the dominant alga available to first-feeding larvae, even though the larvae appeared to consume this algal species. When the *G. polyedra* was swept away by ocean currents and replaced with diatoms, the larvae still starved to death. Consumption of the diatom was probably inhibited by the presence of spines (Lasker 1981). Scura and Jerde (1977) had shown in laboratory feeding trials that one of the dinoflagellates, *Gymnodinium splendens*, that grows in the nursery areas off the coast of California was nutritionally adequate for anchovy larvae, while *G. polyedra* was not. No data on the nutritional composition of these two species were provided.

Similar differences in nutritional value of algal species have been shown to be caused by differences in their content of essential fatty acids. Many marine fish (Cowey et al. 1976; Fujii and Yone 1976; Kitajima and Koda 1976; Kitajima et al. 1979, 1980a, 1980b; Watanabe et al. 1978b, 1983a, 1983b) and crustaceans (Jones et al. 1979; Kanazawa et al. 1977, 1978, 1979a; Levine and Sulkin 1984) require dietary fatty acids of the linolenic (n3) series and frequently have a specific requirement for long-chain (20:5n3 and 22:6n3)[1] members of that series. The marine alga *Dunaliella tertiolecta* contains fatty acids of the n3 series, but none longer than linolenic acid (18:3n3) (Ackman et al. 1968). This species is thus nutritionally deficient for herbivores such as turbot larvae, *Scophthalmus maximus*, that lack the ability to elongate and desaturate these shorter unsaturated fatty acids. This deficiency may be relieved by supplementing a diet containing this alga with a source of 20:5n3 or 22:6n3 (Scott and Middleton 1979). Kanazawa et al. (1979b) have reviewed the literature on the essential fatty acid requirement of aquatic animals and noted a relationship between the specific requirement for 20:5n3 or 22:6n3 and the inability to enzymatically elongate and effectively desaturate 18:3n3 to a longer chain fatty acid. In the case where organisms have this ability, the n3 or n6 fatty acids which originate in plants may be altered as they pass through the various trophic levels. For example, Kayama et al. (1963) suggested that the 18:3n3 of the phytoplankter *Chaetoceros simplex* was elongated to 20:5n3 in the herbivore *Artemia salina* and to 22:6n3 in the guppy, *Lebistes reticulatus*.

The rotifer *Branchionus plicatelis* does not have the ability to convert 18:2n6 or 18:3n3 to longer chain polyunsaturated fatty acids. Though the rotifer can survive on diets such as *C. simplex*, *D. tertiolecta*, or yeast, its growth rate is enhanced by a dietary source of 20:5n3 or 22:6n3 Hirayama and Watanabe 1973; Hirayama and Funamoto 1983). Thus, not only the absence of n3 fatty acids but also the lack of specific long-chain fatty acids may affect organisms on more than one trophic level.

Many species of algae have been evaluated in terms of their nutritional value to molluscs (Walne 1970; Epifanio et al. 1981; Carefoot 1967; C. T. Enright, C. G. Newkirk, J. S. Craigie, and J. D. Castell, unpubl. data). In most cases, however, the components responsible for the difference in nutritional value have not been identified. Growth and survival of the oyster *Crassostrea gigas* was improved significantly when a diet of *D. tertiolecta* was supplemented with microcapsules containing 22:6n3 or oyster lipid (Langdon and Waldock 1981).

Variations in lipid components of algae (Ackman et al. 1968; Alam et al. 1979; Kate and Volcani 1966; Ricketts 1966) have sometimes been identified as one nutritional factor to explain differences in growth and survival of organisms feeding on specific species of phytoplankton. Other nutrients such as vitamins, proteins, essential amino acids, minerals, and carbohydrates as well as the physical characteristics of the food such as cell wall thickness, size, shape, presence of spines, and color may also affect the nutritional value of each algal species.

The chemical composition and hence the nutritional value of a single species of algae varies in response to temperature (Holton et al. 1964; Teshima et al. 1983), dissolved nutrients (Harris et al. 1965; Reitz and Hamilton 1967), light (Nichols 1965), and age (Otsuka and Morimuria 1966; Everhart and Ronkin 1966; Ackman et al. 1964). For example, the total lipid content of the diatom *Cyclotella cryptica* will double under conditions of silicate limitation (Shifrin and Chisholm 1981; Werner 1977). Nitrogen deficiency induced more than a threefold increase in the total lipid (as high as 72% of the dry weight) of *Monallantus salina*. Some of the temporal changes in the chemical compositions of many species of zooplankton are responses to qualitative and quantitative variations in phytoplankton (Gardner and Riley 1972; Kattner et al. 1981; Lee 1974a, 1974b; Mayzaud 1976; Morris 1971; Sargent et al. 1977). This variation in nutrient composition among zooplankton species has been shown to affect the next trophic level as species succession occurs (Takahashi and Yamada 1976).

## Maternal Nutrition

Although nutrition may affect all phases of the lobster's development, nutritional factors that limit successful reproduction might have the most adverse effects on recruitment. The level and composition of the dietary lipid of adults of several species of fish and crustaceans have been shown to have a significant effect on ovarian development, fecundity, and hatchability of eggs. Ohmae et al. (1979) reported a direct relationship between hatchability and the content of 22:6n3 in the lipids of carp eggs. Hatchability decreased when the egg lipids contained less than 10% 22:6n3. Middleditch et al. (1979, 1980) reported that shrimp, *Penaeus setiferus*, require

[1]A deficiency of any one or combination of essential nutrients will result in poor growth and eventually death. For the purposes of this paper we will tend to focus on essential fatty acids, as there are many recent examples of their importance in recruitment. An abbreviated form will be used throughout where the first number represents the number of carbons in the fatty acids, the number following the colon is the number of double bonds, and the number following *n* is the position of the first double bond counting from the methyl end.

20:5n3 or 22:6n3 for ovarian maturation. The universal importance of dietary lipids in reproduction of crustaceans at all latitudes is exemplified by high levels of lipid and polyunsaturated fatty acids in ovaries and eggs of a semitropical prawn, *Penaeus japonicus* (Teshima and Kanazawa 1983), and of the polar shrimp, *Chorismus antarcticus* (Clarke 1982). The importance of essential fatty acids and total lipid levels incorporated into crustacean eggs has been emphasized further by the work of Capuzzo and co-workers at the Woods Hole Oceanographic Institute, Massachusetts. Triglycerides are an important energy reserve during embryonic development (Sasaki 1984; Sasaki et al. 1986). The nutrient reserves at the time of hatching are a function of the initial deposited yolk lipid and the temperature regime to which the egg has been exposed. This triglyceride reserve at hatching affects the time to irreversible starvation (Anger et al. 1985).

Resorption of eggs from ovaries of lobsters can be caused by either starvation or dietary deficiencies of protein or lipid (Castell and Budson 1974; Castell and Covey 1976). The total lipid content of developing lobster ovaries was found to exceed 30% of the tissue wet weight (J. D. Castell et al., unpubl.).

The carotenoid pigments are another group of lipids considered to be important in the production and viability of the eggs of many aquatic animals (Tacon 1981; Harris 1984; Hirao et al. 1954; Mikulin and Soin 1975). Carotenoids cannot be synthesized de novo by animals and must be derived from plant pigments. Hirao et al. (1954) noted a lower concentration of the yellow pigment, violaxanthin, in eggs of rainbow trout, *Salmo gairdneri*, which had lower hatchabilities. Harris (1984) observed a higher incidence of fertile females among rainbow trout fed diets with 20–40 mg canthaxanthin/kg than among those receiving none in the diet. Morrison and Smith (1981) reported that supplementation of dietary carotenoid had no effect on fecundity or egg quality of brook trout, *Salvenlinus fontinalis*. Other reports claim a significant effect of dietary carotenoids on egg production or hatchability (Deufel 1965, 1975; Hubbs and Stavenhagen 1958; Georgiev 1971; Watanabe et al. 1984b). Balon (1979) suggested that the yellow carotenoid pigment in the eggs of the cichlid *Labeotropheus* may perform a respiratory function, especially under conditions of oxygen limitation.

Additional hypotheses for the physiological role of carotenoids have been presented. Anderson et al. (1974) and Tacon (1981) suggested that the carotenoids serve as antioxidants, similar to vitamin E. Hartmann et al. (1947) postulated that astaxanthin in the eggs of rainbow trout acts as a hormone to promote fertilization. The carotenoids are involved in the protective coloration through the whole life cycle of most fish and crustaceans.

Although juvenile and adult lobsters grow and survive through many molts on diets deficient in carotenoids (Conklin et al. 1980; Boghen et al. 1982; Bordner et al. 1983), these pigments may play a role in lobster reproduction. The dark green color of lobster eggs is caused by an astaxanthin–protein complex within the eggs. We have noticed a reduced production of viable larvae from female lobsters with lighter green colored eggs captured from offshore east of Shelburne, Nova Scotia. It is possible that the astaxanthin incorporated in the lobster eggs plays an important function in embryonic development.

The carotenoids such as β-carotene are also vital to survival and reproduction in fish as precursors of vitamin A. Parental vitamin A deficiency reduced survival of darter, *Osteichthyse*, eggs (Hubbs and Stavenhagen 1958) and reduced early embryogenesis in *Salmo irideus* eggs (Georgiev 1971). Mikulin and Soin (1975) observed that vitamin A content in teleost fish increases before spawning and decreases sharply after spawning. They suggested that carotenoids are important in coloration, perception of light, in the process of egg fertilization, protection of eggs against environmental factors, in respiration, in oxidation–reduction reactions, as well as in the formation of vitamin A.

Ascorbic acid is another vitamin associated with ovarian development in fish (Sandnes and Braekken 1981; Hilton et al. 1979). Sandnes et al. (1984) showed that ascorbic acid supplementation of a broodstock diet increased the hatchability of rainbow trout eggs. Tolbert (1979) suggested that ascorbic acids plays a role in regulating steroidogenesis in adrenal glands and gonads. Dietary ascorbic acid may not be as important in lobster broodstock diets, since it has been shown that this vitamin is not required in the diet of juveniles (Kean et al. 1985b). Subadults are capable of de novo synthesis of dehydroascorbic acid from glucose (Desjardins et al. 1985).

Other dietary factors that have been shown to affect fecundity and egg viability include vitamin E in ayu, *Plecoglossus altivelis* (Takeuchi et al. 1981), iron and vitamin $B_2$ in rainbow trout (Hirao et al. 1955), macroelements in rainbow trout (Satia 1974), and protein level and quality in red sea bream, *Pagrus major* (Watanabe et al. 1984a, 1984c).

Finally, limitations in the total quantity of food can be expected to reduce the number of larvae produced, as was shown for *L. reticulatus* (Hester 1964).

## Nutrition of Larvae

The larval stage is the next critical phase of development. Scarratt (1964) had shown that in the northern part of the Northumberland Strait considerable variation existed in abundance and survival of lobster larvae, *H. americanus*. He demonstrated a relationship between stage IV larval abundance and subsequent lobster stocks (Scarratt 1973). Survival of pelagic larvae that do not become prey will depend in part on the nutritional value of the food organisms present. Variations in the predominant species of algal blooms could affect growth and survival of lobster larvae directly as they do anchovy larvae (Lasker 1981) or indirectly by affecting nutritional value and/or type of zooplankton available as food. Much effort was spent trying to find appropriate food organisms for the successful culture of lobster larvae (Carlberg and Van Olst 1976; Ghelardi 1967; Hughes and Matthiessen 1962; Scattergood 1949; Williams 1907), but little research has been directed toward an understanding of nutritional requirements.

## Juvenile Nutrition

Most of the data on lobster nutrition are based on feeding trials conducted with juveniles (fourth to tenth) (Conklin 1975, 1980; Conklin et al. 1983). The fast growth rate during these early stages is conducive to a relatively quick development of deficiency symptoms: failure to molt, reduced growth, molt death syndrome, or high mortality. Additional advantages of working with juveniles are that a larger number of experimental animals can be used and the short intermolt period provides results within a few months compared with the 10 mo to a year or more required with adult lobsters (Castell and Covey 1976).

A purified test diet with casein and egg albumin as protein sources was developed for juvenile lobsters (Conklin 1980). Improved growth and survival were obtained when casein and egg albumin were replaced with a protein from whole, "deshelled" rock crab, *Cancer irroratus* (Boghen et al. 1982; Castell et al. 1985). The protein requirement of lobsters, which had initially been estimated with casein to be from 50 to 60% dry diet (Castell and Budson 1974), appears to be closer to 30% when casein was replaced by crab protein (J. D. Castell, unpubl. results).

Although the quantitative dietary essential amino acid requirements have not yet been determined, Mason and Castell (1980) found that supplementing casein-based diets with essential amino acids improved lobster growth. Gallagher and Brown (1975), using $C^{14}$ radiotracer techniques, demonstrated that lobsters could not synthesize de novo 10 amino acids essential in the diet of most animals.

The rotifer *B. plicatilis*, widely used for the first-feeding larvae of fish and crustaceans (Ito 1960), has been cultured principally with marine algae such as *Chlorella* (Teshima et al. 1981). To reduce the cost of producing live food for fish larval, it was found that rotifers could be grown on baker's yeast (Hirata and Mori 1967). Unfortunately, feeding of yeast-cultured rotifers was associated with high mortality of some fish larvae such as those of red sea bream (Kitajima and Koda 1976). The basis for this mortality was identified as a deficiency of 20:5n3 or 22:6n3 fatty acids in rotifiers that had been fed yeast (Watanabe et al. 1978a).

Similarly, rotifers cultured on the alga *D. tertiolecta* were lacking 20:5n3 or 22:6n3 and were therefore nutritionally deficient for the larvae of the blue crab, *Callinectes sapidus* (Sulkin 1978), and stone crab, *Menippe mercinaria* (Sulkin and van Heukelem 1980). Larvae of the deep sea red crab, *Geryon quinquedens*, were able to compete zoeal development on a diet of only *Dunaliella*-fed rotifers, suggesting that this crustacean can elongate and desaturate 18:3n3 to 22:6n3 (Sulkin and van Henkelem 1980). The essential fatty acid requirements of the larvae of many species have been identified by using rotifer diets (Watanabe et al. 1978a, 1983a, 1983b; Lee et al. 1981; Kitajima et al. 1979, 1980a, 1980b).

Recent research by Sasaki (1984) suggests that polyunsaturated fatty acids may play an important role in the survival and growth of lobster larvae. He found selective sparing of 20:5n3 and 22:6n3 during the lipid catabolic stage of lobster embryonic development. It is expected that variations in the content of many other essential nutrients in prey organisms will influence general health, growth, and survival of lobster larvae.

One of the few nutrition experiments with adult lobsters indicates that lobsters required about 5% of the dry weight of the diet as lipid and that cod liver oil, containing 20:5n3 and 22:6n3, was nutritionally superior to either corn oil (containing 18:2n6) or hydrogenated coconut oil (with saturated fatty acids) (Castell and Covey 1976). An attempt to determine the essential fatty acid requirements of juvenile lobsters (Castell and Boghen 1979) was unsuccessful due to the nutritional inadequacy of casein and the apparent requirement by lobster for 6–7% soy lecithin (Conklin 1980). The soy lecithin used contained about 50% 18:2n6 and 7% 18:3n3, and thus it was not possible to formulate an essential fatty acid deficient diet that contained the required amount of lecithin. When casein and albumin were replaced by purified crab protein, it was found that lecithin was not essential in the juvenile lobster diet (Kean et al. 1985a). This finding has permitted an investigation of the essential fatty acid requirements of juvenile lobsters (K. E. Harrison, Biology Department, Dalhousie University, Halifax, N.S., pers. comm.). Preliminary growth results indicate that dietary 22:6n3 is superior to either 18:2n6 or 18:3n3.

Kean et al. (1985a) confirmed the essentiality of a dietary source of sterol, though they suggested that the requirement might be lower than the 0.5% identified by Castell et al. (1975) in experiments using casein-based diets. D'Abramo et al. (1984) had also suggested that juvenile lobsters have a lower sterol requirement that is partially, and may be totally, specific for cholesterol.

It is assumed that the lobster, like other animal species, requires a dietary source of B vitamins (Conklin et al. 1983). Certainly, pantothenic acid (W. Young-Lai, Marine Lobster Farms Inc., Victoria, P.E.I., unpubl. data) and riboflavin (D. E. Conklin, University of California Bodega Marine Laboratory, Bodega Bay, CA, pers. comm.) are essential in diets for juvenile lobster, though the quantitative requirements for these vitamins have not been determined. Vitamin C, though apparently required by other crustaceans (Margarelli et al. 1979; Deshimaru and Kuroki 1976; Guary et al. 1975; Lightner et al. 1979), is not required by lobsters (Kean et al. 1985b) because lobsters can synthesize it from glucose (Desjardins et al. 1985).

Excess fat-soluble vitamins are stored and it takes a relatively long time for deficiency symptoms to develop. Diets deficient in either vitamin A or D had no significant effect on mortality or growth, even after 21 wk compared with control diets (Castell et al. 1985). Vitamin E deficiency resulted in reduced growth, yellow pigmentation in the exoskeleton, and frequent loss of appendages.

The absence of dietary carotenoids resulted in pale blue to white lobsters; however, good growth and survival are obtained without dietary carotenoids (Conklin 1980; Boghen et al. 1982). The incorporation of astaxanthin from crayfish processing waste or synthetic canthaxanthin in the diet produces more natural pigmentation of juvenile lobsters (D'Abramo et al. 1983).

The presence of most mineral elements in seawater (and the leaching of mineral salts from purified diet pellets) creates difficulties in the determination of quantitative mineral requirements of lobsters. Optimal growth was obtained when a casein/lecithin diet contained 5% of a complex (modified Bernhart–Tomorelli) salt mix (J. D. Castell, unpubl. results). However, quantitative identification of mineral requirements awaits future research efforts. Calcium is important for mineralization of the exoskeleton. Conklin et al. (1983) recommended a Ca/P ratio of 1:2. Copper, an essential constituent of the respiratory protein hemocyanin, is an interesting element, as its content in lobsters demonstrates a linear relationship with silver (Chou and Uthe 1978). When the hepatopancreatic levels of copper increased in response to increasing dietary levels of this mineral, a corresponding increase in silver occurred in this organ (Chou et al. 1985).

Though there is no doubt that qualitative and quantitative nutrient supplies to juveniles are important to their growth and survival, it is probable that nutrition at this stage is least critical to recruitment. The prerecruit phase in *Homarus*, which lasts for 6–8 yr (Wilder 1953), is in sharp contrast with the prerecruit period lasting for 1 or 2 yr for many commercial fish species. This extended prerecruit stage and the ability to survive for relatively long periods with no food permit the juvenile lobster to withstand short-term fluctuations in availability of

food organisms. It is likely that drastic long-term changes in the flora and fauna of an area of the sea bottom, such as the sea urchin caused denuding of large areas of seabed off southeastern Nova Scotia (Mann and Breen 1972), could affect the nutritional status of subadult and adult lobsters inhabiting the area.

## Conclusions and Recommendations

Since the survival and growth of the larval stage is critical to lobster year-class strength (Scarratt 1973), it would be useful to have a method of quantifying the nutritional status of larvae captured from various areas. The RNA/DNA ratio shows an excellent correlation with recent growth rate and nutritional status. It has been applied to the larvae of golden shiner, *Notemigonus crysoleucas* (Bulow 1970), cod, *Gadus morhua* (Buckley 1979), winter flounder, *Pseudopleuronectes americanus* (Buckley 1980, 1982), and sand lance, *Ammodytes americanus* (Buckley et al. 1984), and might be used to evaluate larval lobster nutritional status. A similar relationship between growth rate and the RNA concentration has also been demonstrated in some invertebrates (Sutcliffe 1970). The presumed correlation between the RNA/DNA ratio and nutritional status of lobster larvae could be initially investigated by feeding studies in the laboratory. A formula relating RNA/DNA ratio, feed status, and environmental temperature was developed by Buckley (1984) for larvae of several fish species. A similar formula might be used to estimate recent growth of lobster larvae.

Since essential fatty acids have been shown to be critical in the diet of many fish and crustacean larvae, it will be important to determine the essential fatty acid requirement of lobster larvae. It will then be possible to assess the value of essential fatty acids in the planktonic organisms present in the ocean as natural food for lobster larvae. Though it is unlikely that any nutritional deficiency in food organisms present in the ocean could be rectified, the knowledge might be useful in predicting larval survival in any given area.

Differences in hatchability of eggs of female lobsters brought to the Halifax Fisheries Research Laboratory from the wild over the last 15 yr have been observed (J. D. Castell et al., unpubl.). Most noticeable was the poor hatchability of the eggs with reduced pigmentation on lobsters from offshore in 1984. Though broodstock feeding trials designed to evaluate the effect of nutritional factors such as essential fatty acids and carotenoid pigments on egg production and hatchability would be relatively long term, information gained might be valuable to lobster recruitment studies. Small samples of eggs from wild populations might, on analysis, allow prediction of larval production and a hindcast of the dietary conditions the parents had experienced.

These are a few of the possible applications of nutrition research to lobster recruitment theory, modelling exercises, and year-class strength estimation.

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## References

ACKMAN, R. G., P. M. JANGAARD, R. J. HOYLE, AND H. BROCKERHOFF. 1964. Origin of marine fatty acids. I. Analysis of the fatty acids produced by the diatom *Skeletonema costatum*. J. Fish. Res. Board Can. 21: 747–756.

ACKMAN, R. G., C. S. TOCHER, AND J. MCLACHLAN. 1968. Marine phytoplankter fatty acids. J. Fish. Res. Board Can. 25: 1603–1620.

ALAM, M., T. B. SANSING, E. L. BUSBY, D. R. MARTINIZ, AND S. M. RAY. 1979. Dinoflagellate sterols. I: Steroid composition of the dinoflagellates of *Gonyaulax* species. Steroids 33: 197–203.

ANDERSON, S. M., N. I. KRINSKY, M. J. STONE, AND D. C. CLAGETT. 1974. Effect of singlet oxygen quenchers on oxidative damage to liposomes initiated by photosensitization or by radiofrequency discharge. Photochem. Photobiol. 20: 65–69.

ANGER, K., V. STORCH, V. ANGER, AND J. M. CAPUZZO. 1985. Effects of starvation on molt cycle and hepatopancrease of Stage I lobster larvae (*Homarus americanus*). Helgol. Meersunters. 39: 107–116.

BALON, E. K. 1979. Early ontogeny of *Labeotropheus* Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. Environ. Bull. Fish. 2: 147–176.

BLAXTER, J. H. S., AND G. HEMPEL. 1963. The influence of egg size on herring larvae. J. Cons. Int. Explor. Mer 28: 211–240.

BOGHEN, A. D., J. D. CASTELL, AND D. E. CONKLIN. 1982. In search of a reference protein to replace "vitamin-free casein" in lobster nutrition studies. Can. J. Zool. 60: 2033–2038.

BORDNER, C. E., L. R. D'ABRAMO, AND D. E. CONKLIN. 1983. Assimilation of nutrients by cultured hybrid lobsters (*Homarus* sp.) fed experimental diets. J. World Maricult. Soc. 14: 11–24.

BUCKLEY, L. J. 1979. Relationships between RNA–DNA ratio, prey density, and growth rate in Atlantic cod (*Gadus morhua*) larvae. J. Fish. Res. Board Can. 36: 1497–1502.

1980. Changes in ribonucleic acid, deoxyribonucleic acid and protein content during ontogenesis in winter flounder, *Pseudopleuronectes americanus*, and the effect of starvation. Fish. Bull. U.S. 77: 703–708.

1982. Effects of temperature on growth with biochemical composition of larval winter flounder (*Pseudopleuronectes americanus*). Mar. Ecol. Prog. Ser. 8: 181–186.

1984. RNA–DNA ratio: an index of larval fish growth in the sea. Mar. Biol. 80: 291–298.

BUCKLEY, L. J., S. I. TURNER, T. A. HALAVIK, A. S. SMIGIELSKI, S. M. DREW, AND G. C. LAURENCE. 1984. Effects of temperature and food availability on growth, survival and RNA-DNA ratio of larval sand lance (*Ammodytes americanus*). Mar. Ecol. Prog. Ser. 15: 91–97.

BULOW, F. J. 1970. RNA-DNA ratios as indicators on recent growth rates of a fish. J. Fish. Res. Board Can. 27: 2343–2349.

CAREFOOT, T. H. 1967. Growth and nutrition of *Aplysia punctata* feeding on a variety of marine algae. J. Mar. Biol. Assoc. U.K. 47: 565–570.

CARLBERG, J. M., AND J. C. VAN OLST. 1976. Brine shrimp (*Artemia salina*) consumption by the larval stages of the American lobster (*Homarus americanus*) in relation to food density and water temperature. Proc. World Maricult. Soc. 7: 379–389.

CASTELL, J. D., AND A. D. BOGHEN. 1979. Fatty acid metabolism in juvenile lobster (*Homarus americanus*) fed a diet low in methionine and histidine. Proc. World Maricult. Soc. 10: 720–727.

CASTELL, J. D., AND S. D. BUDSON. 1974. The effect on *Homarus americanus* of dietary protein levels. J. Fish. Res. Board Can. 31: 1363–1370.

CASTELL, J. D., AND J. F. COVEY. 1976. Dietary lipid requirements of adult lobsters, *Homarus americanus* (M.E.). J. Nutr. 106: 1159–1165.

CASTELL, J. D., J. C. KEAN, AND M. E. SCHENK. 1985. Lipid soluble vitamin requirements of juvenile American lobster (*Homarus americanus*). Abstracts of the 16th Annual Meeting of the World Mariculture Society, Orlando, Florida, January 13–18, 1985.

CASTELL, J. D., E. G. MASON, AND J. F. COVEY. 1975. Cholesterol requirements of the juvenile lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 32: 1431–1435.

CHOU, C. L., J. F. UTHE, J. D. CASTELL, AND J. C. KEAN. 1985. Heavy metal interactions in juvenile American lobster (*Homarus americanus*). Can. Tech. Rep. Fish. Aquat. Sci. 2368: 21 p.

CHOU, C. L., AND J. F. UTHE. 1978. Heavy metal relationships in lobster (*Homarus americanus*) and rock crab (*Cancer irroratus*) digestive glands. I.C.E.S. Statutory Meeting Report C.M. 1978/E:15: 8 p.

CLARKE, A. 1982. Lipid synthesis and reproduction in the polar shrimp *Chorismus antarcticus*. Mar. Ecol. Prog. Ser. 9: 81–90.

CONKLIN, D. E. 1975. Nutritional studies of lobster (*Homarus americanus*), p. 287–296. *In* K. S. Price, W. N. Shaw, and K. S. Danberg [ed.] Proc.

First Int. Conf. Aquacult. Nutr., College of Marine Sciences, University of Delaware, Newark, DE.

1980. Nutrition, p. 277–300. *In* S. J. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. I. Academic Press, New York, NY.

CONKLIN, D. E., L. R. D'ABRAMO, C. E. BORDNER, AND N. A. BAUM. 1980. A successful purified diet for the culture of juvenile lobsters: the effect of lecithin. Aquaculture 21: 243–249.

CONKLIN, D. E., L. R. D'ABRAMO, AND K. NORMAN-BOUDREAU. 1983. Lobster nutrition, p. 413–423. *In* J. P. McVey [ed.] Handbook of mariculture. Vol. 1. Crustacean aquaculture. CRC Press, Inc., Boca Raton, FL.

COWEY, C. B., J. M. OWEN, J. W. ADRON, AND C. MIDDLETON. 1976. Studies on the nutrition of marine flatfish. The effect of different dietary fatty acids on the growth and fatty acid composition of turbot (*Scophthalmus maximux*). Br. J. Nutr. 36: 479–486.

CUSHING, D. H. 1973. Recruitment and parent stock in fishes. WSG 73-1. Division of Marine Research, University of Washington, Seattle, WA. 97 p.

D'ABRAMO, L. R., N. A. BAUM, C. E. BORDNER, AND D. E. CONKLIN. 1983. Carotenoids as a source of pigmentation in juvenile lobsters fed a purified diet. Can. J. Fish. Aquat. Sci. 40: 699–704.

D'ABRAMO, L. R., C. E. BORDNER, D. E. CONKLIN, AND N. A. BAUM. 1984. Sterol requirement of juvenile lobster, *Homarus* sp. Aquaculture 42: 13–25.

DESHIMARU, O., AND K. KUROKI. 1976. Studies on a purified diet for prawn — vii. Adequate dietary levels of ascorbic acid and inositol. Bull. Jpn. Soc. Sci. Fish. 42: 571–576.

DESJARDINS, L. M., J. D. CASTELL, AND J. C. KEAN. 1985. Synthesis of dehydroascorbic acid by subadult lobsters (*Homarus americanus*). Can. J. Fish. Aquat. Sci. 42: 370–373.

DEUFEL, J. 1965. Pigmentierungsversuche mit canthaxanthin bëi regenbogenforellen. Arch. Fischereiwiss. 16: 125–132.

1975. Physiologische wirkungen von carotenoiden bëi salmoniden. Schwiez. Z. Hydrol. 37: 244–248.

EPIFANIO, C. E., C. C. VELENTI, AND C. L. TURK. 1981. A comparison of *Phaedoctyloum tricornatum* and *Thalassiosira pseudonama* as foods for the oyster, *Crassostrea virginica*. Aquaculture 23: 347–353.

EVERHART, L. P. JR., AND R. R. RONKIN. 1966. Changes in the lipids of cells from aging populations of *Tetrahymena pyriformis*. J. Protozool. 13: 646–650.

FUJII, M., AND Y. YONE. 1976. Studies on nutrition of red sea bream. XIII. Effect of dietary linolenic acid and w3 polyunsaturated fatty acids on growth and feed efficiency. Bull. Jpn. Soc. Sci. Fish. 42: 583–588.

GALLAGHER, M. L., AND D. W. BROWN. 1975. Amino acid requirements of the lobster. Fed. Proc. 34: 880.

GARDNER, D., AND J. P. RILEY. 1972. Seasonal variation in the component fatty acid distribution of the lipids of *Balanus balanoides*. J. Mar. Biol. Assoc. U.K. 52: 839–845.

GEORGIEV, G. S. 1971. Carotenoids and vitamin A content in *Salmon irideus* eggs and their significance in the initial period of the embryogenesis. Folia Balc. 2: 1–10.

GHELARDI, R. J. 1967. Progress report on the 1965 and 1966 lobster introductions at Fatty Basin, Vancouver Island, British Columbia. J. Fish. Res. Board Can. Tech. Rep. 44: 40 p.

GUARY, M. M., H. J. CECCALDI, AND A. KANAZAWA. 1975. Variations de tout d'acide ascorbique au Cours de développment de l'ovaire et du cycle d'intermue chez *Palaemon serratus*. Mar. Biol. 32: 349–355.

HARRIS, L. E. 1984. Effects of a broodfish diet fortified with canthaxanthin on female fecundity and egg color. Aquaculture 43: 179–183.

HARRIS, R. V., P. HARRIS, AND A. T. JAMES. 1965. The fatty acid metabolism of *Chlorella valgaris*. Biochim. Biophys. Acta 106: 465–473.

HARTMANN, F., F. G. MERDEM, R. KUHN, AND H. J. BEIHLIG. 1947., Über die gynogamone der regenbogen Florelle (Concerning the gynogamone in rainbow trout). Naturwissenschaft 34: 23–26.

HESTER, F. J. 1964. Effects of food supply on fecundity in the female guppy, *Lebistes reticulatus* (Peters). J. Fish. Res. Board Can. 21. 757–764.

HILTON, J. W., C. Y. CHOU, R. G. BROWN, AND S. S. SLINGER. 1979. The synthesis, half-life and distribution of ascorbic acid in rainbow trout. Comp. Biochem. Physiol. 563A: 447–453.

HIRAO, S., J. YAMADA, AND R. KIKUCKI. 1954. Violaxanthin in rainbow trout eggs. Bull. Jpn. Soc. Sci. Fish. 20: 431–434.

1955. Relationship between chemical constituents of rainbow trout eggs and the hatching rate. Bull. Jpn. Soc. Sci. Fish. 21: 240–243.

HIRATA, H., AND Y. MORI. 1967. Saibai-Gyogyo 5: 36–40. (cf. Teshima, S. i., A. Kanazawa, N. Kamezaki, and H. Hirata. 1981. Fatty acids and sterol components of the rotifer cultured by a feedback system. Bull. Jpn. Soc. Sci. Fish. 47: 515–521)

HIRAYAMA, I. K., AND H. FUNAMOTO. 1983. Supplementary effect of several nutrients on nutritive deficiency of Baker's yeast for population growth of the rotifer *Brachionus plicatilis*. Bull. Jpn. Soc. Sci. Fish. 49: 505–510.

HIRAYAMA, K., AND K. WATANABE. 1973. Fundamental studies on physiology of rotifer for its mass culture — IV. Nutritional effects of yeast on population growth of rotifers. Bull. Jpn. Soc. Sci. Fish. 39: 1129–1133.

HJORT, J. 1914. Fluctuations in the great fisheries of Northern Europe. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 20: 1–228.

HOLTON, R. W., H. BLECKER, AND M. ONERE. 1964. Effect of growth temperature on the fatty acid composition of a blue-green alga. Photochemistry 3: 595–602.

HUBBS, C., AND L. STAVENHAGEN. 1958. Effects of maternal carotenoid deficiency on the viability of darter (*Osteichthyse*) offspring. Physiol. Zool. 31: 280–283.

HUGHES, J. T., AND G. C. MATTHIESSEN. 1962. Observations on the biology of the American lobster, *Homarus americanus*. Limnol. Oceanogr. 7: 414–421.

HUNTER, J. R. [ED.] 1976. Report of a colloquium on larval fish mortality studies and their relation to fishery research, January 1975. NOAA Tech. Rep. Circ. No. 395: 5 p.

ITO, T. 1960. On the Culture of the mixohaline rotifer, *Brachionus plicatilis* O. F. Muller, in seawater. Rep. Fac. Fish. Prefect Univ. Mie 3: 708–740.

JONES, D. A., A. KANAZAWA, AND U. ONO. 1979. Studies on the nutritional requirements of the larval stages of *Penaeus japonicus* using microencapsulated diets. Mar. Biol. 54: 262–267.

KANAZAWA, A., S. i. TESHIMA, AND M. ENDO. 1979a. Requirements of prawn, *Penaeus japonicus*, for essential fatty acids. Mem. Fac. Fish. Kagashima Univ. 28: 27–33.

KANAZAWA, A., S. i. TESHIMA, M. ENDO, AND M. KAYAMA. 1978. Effect of eicosapentaenoic acid on growth and fatty acid composition of the prawn, *Penaeus japonicus*. Mem. Fac. Fish. Kagoshima Univ. 27: 35–40.

KANAZAWA, A., S. i. TESHIMA, AND K. ONO. 1979b. Relationship between essential fatty acid requirements of aquatic animals and the capacity for bioconversion of linolenic acid to highly unsaturated fatty acids. Comp. Biochem. Physiol. 63B: 295–298.

KANAZAWA, A., S. i. TESHIMA, AND S. TOKIWA. 1977. Nutritional requirements of prawn — VIII. Effect of dietary lipids on growth. Bull. Jpn. Soc. Sci. Fish. 43: 849–856.

KATE, M., AND B. E. VOLCANI. 1966. Lipid components of diatoms. Biochim. Biophys. Acta 116: 264–278.

KATTNER, G., M. KRAUSE, AND J. TRAHMS. 1981. Lipid composition of some typical North Sea copepods. Mar. Ecol. Prog. Ser. 4: 69–74.

KAYAMA, M., Y. TSUCHIYA, AND J. F. MEAD. 1963. A model experiment of an aquatic food chain with special significance in fatty acid conversion. Bull. Jpn. Soc. Sci. Fish. 29: 452–458.

KEAN, J. C., J. D. CASTELL, A. G. BOGHEN, L. R. D'ABRAMO, AND D. E. CONKLIN. 1985a. A reevaluation of the lecithin and cholesterol requirements of juvenile lobsters (*Homarus americanus*) using crab protein based diets. Aquaculture 47: 143–149.

KEAN, J. C., J. D. CASTELL, AND D. J. TRIDER. 1985b. Juvenile lobster (*Homarus americanus*) do not require dietary ascorbic acid. Can. J. Fish. Aquat. Sci. 42: 368–370.

KITAJIMA, C., T. ARAKAWA, F. OOWA, S. FUJITA, O. IMADA, T. WATANABE, AND Y. YONE. 1980a. Dietary value for red sea bream larvae of rotifer *Brachionus plicatilis* cultured with a new type of yeast. Bull. Jpn. Soc. Sci. Fish. 46: 43–46.

KITAJIMA, C., S. FUJITA, F. OHWA, Y. YONE, AND T. WATANABE. 1979. Improvements of dietary value for red sea bream larvae of rotifers *Brachionus plicatilis* cultured with Baker's yeast *Saccharomyces cerevisiae*. Bull. Jpn. Soc. Sci. Fish. 45: 469–471.

KITAJIMA, C., AND T. KODA. 1976. Lethal effects of the rotifer cultured with Baker's yeast on the larval red sea bream, *Pagrus major*, and the increase rate using the rotifer reared with *Chlorella* sp. Bull. Nagasaki Pref. Inst. Fish. 2: 113–116.

KITAJIMA, C., M. YOSHIDA, AND T. WATANABE. 1980b. Dietary value for ayu *Plecoglossus altivelis* of rotifer, *Brachionus plicatilis*, cultured with Baker's yeast *Saccharomyces cerevisiae* supplemented with cuttlefish liver oil. Bull. Jpn. Soc. Sci. Fish. 46: 47–50.

LANGDON, C. J., AND M. J. WALDOCK. 1981. The effect of algal and artificial diets on the growth and fatty acid composition of *Crassostrea gigas* spat. J. Mar. Biol. Assoc. U.K. 61: 431–448.

LASKER, R. 1981. Factors contributing to variable recruitment of the Northern anchovy (*Engraulis mordax*) in the California current: contrasting years

1975 through 1978. *In* R. Lasker and K. Sherman [ed.] The early life history of fish: recent studies. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 198: 375–388.

LASKER, R., AND P. E. SMITH. 1977. Estimation of the effects of environmental variations on the eggs and larvae of the Northern anchovy. Calif. Coop. Oceanic Fish. Invest. Rep. 19: 128–137.

LEE, C. S., F. HU, AND R. HIRANO. 1981. Organisms suitable as food for larvae of black sea bream (*Mylio macrocephalus*). Prog. Fish-Cult. 43: 121–124.

LEE, R. F. 1974a. Lipid composition of the copepod *Calanus hyperboreas* from Arctic Ocean, changes with depth and season. Mar. Biol. 26: 313–318.

1974b. Lipids of zooplankton from Bute Inlet, British Columbia. J. Fish. Res. Board Can. 31: 1577–1582.

LEVINE, D. M., AND S. D. SULKIN. 1984. Nutritional significance of long-chain polyunsaturated fatty acids to the local development of the Brachyuran crab *Eurypanopeus depressus* (Smith). J. Exp. Mar. Biol. Ecol. 81: 211–223.

LIGHTNER, D. V., B. HUNTER, P. C. MARGARELLI, JR., AND L. B. COLVIN. 1979. Ascorbic acid: nutritional requirement and role in wound repair in penaeid shrimp. Proc. World Maricult. Soc. 10: 513–528.

MANN, K. H., AND R. A. BREEN. 1972. The relationship between lobster abundance, sea urchins, and kelp beds. J. Fish. Res. Board Can. 29: 603–605.

MARGARELLI, P. C. J., B. HUNTER, D. V. LIGHTNER, AND L. B. COLVIN. 1979. Black death: an ascorbic acid deficiency disease in penaeid shrimp. J. Biochem. Physiol. 63A: 103–108.

MASON, E. G., AND J. D. CASTELL. 1980. Essential amino acid diets for American lobsters, *Homarus americanus*, using purified amino acid test diets. Proc. World Maricult. Soc. 11: 346–354.

MAYZAUD, P. 1976. Respiration and nitrogen excretion of zooplankton. IV. The influence of starvation on the metabolism and the biochemical composition of some species. Mar. Biol. 37: 47–58.

MCGURK, M. D. 1984. Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. Mar. Biol. 84: 13–26.

MIDDLEDITCH, B. S., S. R. MISSLER, AND H. B. HINES. 1980. Metabolic profiles of shrimp: dietary lipids and ovarian maturation. J. Chromatogr. 195: 359–368.

MIDDLEDITCH, B. S., S. R. MISSLER, D. G. WARD, J. B. MCVEY, A. BROWN, AND A. L. LAWRENCE. 1979. Maturation of penaeid shrimp: dietary fatty acids. Proc. World Maricult. Soc. 10: 472–476.

MIKULIN, A. Y., AND S. G. SOIN. 1975. The functional significance of carotenoids in the embryonic development of teleosts. J. Ichthyol. 15: 749–759.

MORRIS, R. J. 1971. Variation in the fatty acid composition of oceanic euphausids. Deep-Sea Res. 18: 525–529.

MORRISON, J. K., AND C. E. SMITH. 1981. The effects of dietary carotenoid supplementation on egg quality of brook trout. Int. Leafl. 19, Fish. Dev. Center, Bozeman, MT. 6 p.

NICHOLS, B. W. 1965. Light induced changes in the lipids of *Chlorella vulgaris*. Biochim. Biophys. Acta 106: 274–279.

OHMAE, H., R. SUZUKI, AND Y. SHIMMA. 1979. Influence of single cell protein feeds on the growth and reproductivity of carp with reference to fatty acid composition, p. 63–73. *In* J. Habver and K. Tiews [ed.] Finfish nutrition and fishfeed technology. Heenemann, Berlin.

OTSUKA, H., AND Y. MORIMURIA. 1966. Changes of fatty acid composition of *Chlorella ellipsoida* during its cell cycle. Plant Cell Physiol. 7: 663–670.

REITZ, R. C., AND J. G. HAMILTON. 1967. Fatty acid concentrations in synchronous cultures of *Chlorelloa pyrenoidosa*, grown in the presence and absence of glucose. Lipids 2: 381–389.

RICKETTS, T. R. 1966. On the chemical composition of some unicellular algae. Phytochemistry 5: 67–76.

SANDNES, K., AND O. R. BRAEKKEN. 1981. Ascorbic acid and the reproductive cycle of ovaries in cod (*Gadus morhua*). Comp. Biochem. Physiol. 70A: 545–546.

SANDNES, K., Y. ULGENES, O. R. BRAEKKAN, AND F. UTNE. 1984. The effect of ascorbic acid supplementation in broodstock feed on reproduction of rainbow trout (*Salmo gairdneri*). Aquaculture 43: 167–177.

SARGENT, J. R., R. R. GATTEN, E. D. S. CORNER, AND C. C. KILVINGTON. 1977. On the nutrition and metabolism of zooplankton — XI. Lipids in *Calanus helgolandicus* grazing *Biddulphia sinesis*. J. Mar. Biol. Assoc. U.K. 57: 525–533.

SASAKI, G. C. 1984. Biochemical changes associated with embryonic and larval development in the American lobster *Homarus americanus* Milne Edwards. Ph.D. thesis, Massachusetts Institute of Technology and the Woods Hole Oceanographic Institute, Woods Hole, MA. 457 p. (MIT/WHOI-84-8)

SASAKI, G. C., J. M. CAPUZZO, AND P. BIESIOT. 1986. Nutritional and bioenergetic considerations in the development of the American lobster *Homarus americanus*. Can. J. Fish. Aquat. Sci. 43: 2311–2319.

SATIA, B. P. 1974. Growth and reproduction responses of rainbow trout (*Salmo gairdneri*) to different diets. Ph.D. thesis, University of Washington, Seattle, WA. (Microfilm No. AAD74-15525. 1974. Diss. Abst. Int. B. 35: 9)

SCARRATT, D. J. 1964. Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. J. Fish. Res. Board Can. 21: 661–680.

1973. Abundance, survival, and vertical and diurnal distribution of lobster larvae in Northumberland Strait, 1962–63, and their relationship with commercial stocks. J. Fish. Res. Board Can. 30: 1819–1824.

SCATTERGOOD, L. W. 1949. Translations of foreign literature concerning lobster culture and early life history of the lobster. U.S. Fish. Wildl. Serv. Spec. Sci. Rep. Fish. 6: 173 p.

SCOTT, A. P., AND C. MIDDLETON. 1979. Unicellular algae as a food for turbot (*Scophthalmus maximus* L.) larvae. The importance of dietary long-chain polyunsaturated fatty acid. Aquaculture 18: 227–240.

SCURA, E. D., AND C. W. JERDE. 1977. Various species of phytoplankton as food for larval Northern anchovy, *Engralis mordax*, and relative nutritional value of dinoflagellates *Gymnodinium splendens* and *Gonyaulax polyedra*. Fish Bull. U.S. 75: 577–583.

SHIFRIN, W. S., AND S. W. CHISHOLM. 1981. Phytoplankton lipids: interspecific differences and effects of nitrate, silicate and light–dark cycles. J. Phycol. 17: 374–384.

SULKIN, S. D. 1978. Nutritional requirements during larval development of the potunid crab, *Callinectes sapidus* Rathbun. J. Exp. Mar. Biol. Ecol. 34: 29–41.

SULKIN, S. D., AND W. F. VAN HENKELEM. 1980. Ecological and evolutionary significance of nutritional flexibility in planktonic larvae of the deep sea red crab, *Geryon quinquedens* and the stone crab, *Menippe mercinaria*. Mar. Ecol. Prog. Ser. 2: 91–95.

SUTCLIFFE, W. H. JR. 1970. Relationship between growth rate and ribonucleic acid concentration in some invertebrates. J. Fish. Res. Board Can. 27: 606–609.

TACON, A. G. J. 1981. Speculative review of possible carotenoid function in fish. Prog. Fish-Cult. 43: 205–208.

TAKAHASHI, H., AND M. YAMADA. 1976. Lipid composition of seven species of crustacean plankton. Bull. Jpn. Soc. Sci. Fish. 42: 769–776.

TAKEUCHI, M., S. ISHII, AND T. OGISO. 1981. Effect of dietary vitamin E on growth, vitamin E distribution and mortalities of the fertilized eggs and fry in ayu, *Plecoglossus altivelis*. Bull. Tokai Reg. Fish. Res. Lab. 104: 111–120.

TESHIMA, S. i., AND A. KANAZAWA. 1983. Variation in lipid composition during the ovarian maturation of the prawn. Bull. Jpn. Soc. Sci. Fish. 49: 957–962.

TESHIMA, S. i., A. KANAZAWA, N. KAMEZAKI, AND H. HIRATA. 1981. Fatty acids and sterol components of the rotifer cultured by a feedback system. Bull. Jpn. Soc. Sci. Fish. 47: 515–521.

TESHIMA, S. i., S. YAMASAKI, A. KANAZAWA, AND H. HIRATA. 1983. Effects of water temperature and salinity on eicosapentaenoic acid level of marine *Chlorella*. Bull. Jpn. Soc. Sci. Fish. 49: 805.

TOLBERT, B. M. 1979. Ascorbic acid metabolism and physiological function. *In* A. Hanck and G. Ritzel [ed.] Vitamin C: recent advances and aspects in virus diseases, cancer and lipid metabolism. Int. J. Vit. Nutr. Res. Suppl. No. 19: 127–142.

WALNE, P. R. 1970. Studies on the food value of nineteen genera of algae to juvenile bivalves of the genera *Ostrea, Crassostrea, Mercenaria* and *Mytilus*. Fish. Invest. Lond. Ser. 2, Vol. 26: 62 p.

WATANABE, T., A. ITOH, C. KITAJIMA, AND S. FUJITA. 1984a. Effect of dietary protein levels on reproduction of red sea bream. Bull. Jpn. Soc. Sci. Fish. 50: 1015–1022.

WATANABE, T., A. ITOH, A. MURAKAMI, Y. TSUKASHIMA, C. KITAJIMA, AND S. FUJITA. 1984b. Effect of nutritional quality of diets given to broodstock on the verge of spawning on reproduction of red sea bream. Bull. Jpn. Soc. Sci. Fish. 50: 1023–1028.

WATANABE, T., C. KITAJIMA, T. ARAKAWA, K. FUKUSHO, AND S. FUJITA. 1978a. Nutritional quality of rotifer *Brachionus plicatelis* as a living feed from the viewpoint of essential fatty acids for fish. Bull. Jpn. Soc. Sci. Fish. 44: 1109–1114.

WATANABE, T., C. KITAJIMA, AND S. FUJITA. 1983a. Nutritional values of live organisms used in Japan for mass propagation of fish: a review. Aquaculture 34: 115–143.

WATANABE, T., S. OHNASHI, A. ITOH, C. KITAJIMA, AND S. FUJITA. 1984c. Effect of nutritional composition of diet on chemical components of red sea bream broodstock and egg production. Bull. Jpn. Soc. Sci. Fish. 50: 503–515.

WATANABE, T., F. OOWA, C. KITAJIMA, AND S. FUJITA. 1978b. Nutritional quality of brine shrimp, *Artemia salina*, as a living feed from the viewpoint of essential fatty acids for fish. Bull. Jpn. Soc. Sci. Fish. 44: 1115–1121.

WATANABE, T., T. TAMIYA, A. OKA, M. HIRATA, C. KITAJIMA, AND S. FUJITA. 1983b. Improvement of dietary value of live foods for fish larvae by feeding them on w3 highly unsaturated fatty acids and fat-soluble vitamins. Bull. Jpn. Soc. Sci. Fish. 49: 471–479.

WERNER, D. 1977. Silicate metabolism, p. 110–149. *In* W. Warner [ed.] The biology of diatoms. Blackwell Scientific Publications, London.

WILDER, D. G. 1953. The growth rate of the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 10: 371–412.

WILLIAMS, L. W. 1907. The stomach of the lobster and the food of larval lobster, p. 20–178. *In* The Thirty-seventh Annual Report of the Commissioners of Inland Fisheries, Providence, Rhode Island.

# Session 8
# Models of Stock–Recruitment Relationships

Chairman: M. J. Fogarty

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# Modelling Stock–Recruitment Processes in Crustacea: Some Practical and Theoretical Perspectives

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Caddy, J. F. 1986 Modelling stock–recruitment processes in Crustacea: some practical and theoretical perspectives. Can. J. Fish. Aquat. Sci. 43: 2330–2344.

Several approaches toward development of stock and recruitment models for exploited crustacean populations are reviewed. Such approaches include modifications of classical stock–recruitment models, or ones more directly related to crustacean biology. The latter are believed to offer the most promise for practical application. Standard yield per recruit models using continuous growth functions have been applied to crustacean stocks, but moult increment – frequency versions of yield per recruit calculations better reflect the discrete growth in crustaceans and changes in growth on maturity. They can be extrapolated easily to calculate fecundity per recruit and assess the impact of exploitation on spawning potential. Simple, semiquantitative approaches, such as life history tables, promote investigation of hypotheses of growth, mortality, maturity/fecundity, and harvesting strategy on management, but like yield per recruit models, cannot easily take into account density-dependent recruitment. We may look forward to the development of models that take into account the nature of crustacean life histories, reflecting the need for cross-scheduling of growth and reproduction in environmentally limiting conditions. Modelling life history processes in biological time units related to moult cycle duration, and cross-converting to real time for consideration of the fisheries component, should offer a notable simplification of the modelling process. The existence of several "choices" for an individual crustacean at different points in the moulting/reproduction cycles makes cohort models cumbersome and seems to require the adoption of a stochastic approach, for instance Markov-related processes, which better take into account complexities of biology and fishery-related processes. For many crustaceans, recruitment is believed to be subject to a "bottleneck" somewhere subsequent to the early larval stages, and identification of the species niche for postlarval stages could be of great practical importance for management and stock enhancement. The concept of the fractal surface as a postlarval and juvenile habitat is suggested as a promising approach, and an expression for natural mortality at size is derived for obligate crevice dwellers on a fractal surface. In relatively few circumstances for Crustacea have density-dependent factors been demonstrated in the field as affecting spawning success and the survival to recruitment of postlarval and juvenile stages. Recruit survival appears to be dominated by environmental conditions that vary significantly; seasonal timing of larval release depending on environmental change from year to year. Short-cutting the investigation of precise impacts of stock density, fishing effort, and environment on recruitment can be achieved using production models, delayed recruitment models, models with autoregressive terms, or production models using mortality rates, where effort definition is difficult and catchability a function of behaviour and environnment. The overriding influence of environment on recruitment success is illustrated for both short- and long-lived species in the tropics and northern latitudes, and this is especially true for high unit value Crustacea resources whose heavily exploited fisheries generally operate at low spawning stock sizes. Fluctuating predator density, or other multispecies interactions, affect recruitment and available number of niches, and modelling of trophic relationships has promise. The range of possible models corresponds to various degrees of refinement of the data base, and the importance of biotic, abiotic, and geographical factors in controlling crustacean recruitment is stressed. Also of fundamental importance are the economics of exploitation of species with a high and elastic demand, which results in high actual and latent levels of effort, fisheries heavily dependent on incoming year-classes, and serious problems in maintaining exploitation rates at reasonable levels.

Nous examinons plusieurs méthodes concernant la mise au point de modèles des stocks et du recrutement pour des populations exploitées de crustacés. Ces méthodes peuvent être des versions modifiées des modèles classiques de recrutement des stocks, ou d'autres portant plus directement sur la biologie des crustacés. Ce sont ces dernières qui semblent offrir les meilleures possibilités d'application pratique. Des modèles standard du rendement par recrue, fondés sur des fonctions de la croissance continue, ont été appliqués aux stocks de crustacés, mais des versions de ces modèles tenant compte de la fréquence de la mue et de l'accroissement à la mue représentent mieux le caractère discret de la croissance chez les crustacés et des changements dans la croissance à la maturité. Il est alors facile d'extrapoler pour calculer la fécondité par recrue et évaluer l'effet de l'exploitation sur le potentiel reproducteur. Les méthodes simples et semi-quantitatives, comme les tables du cycle biologique, permettent d'examiner les hypothèses sur la croissance, la mortalité, la maturité et la fécondité, ainsi que sur la stratégie d'exploitation, mais, comme les modèles du rendement par recrue, elles ne peuvent rendre facilement compte du recrutement dépendant de la densité. Nous pouvons envisager la mise au point de modèles tenant compte de la nature du cycle biologique des crustacés, et de la nécessité de faire recouper la croissance et la reproduction en fonction des facteurs limitants représentés par les conditions environnementales. En modélisant les processus biologiques en termes d'unités de temps biologique correspondant à la durée du cycle de mue, et en les reconvertissant en temps réel pour tenir compte de l'aspect pêche, on devrait pouvoir simplifier fortement le processus de modélisation. L'existence de plusieurs « choix » pour un seul crustacé à différents points des cycles de mue et de reproduction rend peu pratique l'emploi des modèles par cohortes et semble exiger l'adoption d'une méthode stochastique (par exemple les démarches de type markovien), qui tienne mieux compte

de la complexité des processus biologiques et halieutiques. Chez de nombreux crustacés, il semble que le recrutement soit soumis à un « goulot d'étranglement » à un moment donné après les premiers stades larvaires, et il pourrait être très intéressant sur le plan pratique, pour la gestion et la mise en valeur des stocks, de définir la niche de l'espèce aux stades post-larvaires. L'appel à la surface fractale pour étudier l'habitat des post-larves et des juvéniles semble prometteur, et on obtient une expression de la mortalité naturelle en fonction de la taille pour les habitants obligés des fissures sur la surface fractale. Dans des cas relativement peu nombreux, on a démontré sur le terrain, chez les crustacés, que des facteurs dépendants de la densité affectent le succès de reproduction et la survie jusqu'au recrutement des stades post-larvaires et juvéniles. La survie des recrues semble régie par les conditions environnementales, qui varient de façon importante et, d'une année à l'autre, la libération des larves a lieu à une période différente selon ces conditions. Il est possible d'abréger l'étude des effets précis de la densité des stocks, de l'effort de pêche et de l'environnement sur le recrutement en utilisant des modèles de production, des modèles de recrutement retardé, des modèles avec termes autorégressifs ou des modèles de production utilisant les taux de mortalité, lorsqu'il est difficile de définir l'effort et lorsque la capturabilité est fonction du comportement et de l'environnement. L'influence prépondérante de l'environnement sur le succès de recrutement est illustré pour des espèces à courte et à longue vie sous les tropiques et sous des latitudes nordiques, et cela est particulièrement vrai pour les ressources de crustacés à forte valeur unitaire dont les pêcheries, très exploitées, présentent généralement un faible stock de géniteurs. Les variations dans la densité des prédateurs, ou d'autres interactions plurispécifiques, affectent le recrutement et le nombre de niches disponibles, et la modélisation des relations trophiques est prometteuse. La gamme des modèles possibles correspond à divers degrés de précision de la base de données, et nous mettons l'accent sur l'importance des facteurs biotiques, abiotiques et géographiques dans le recrutement des crustacés. Autre question fondamentale, l'économique de l'exploitation des espèces présentant une demande forte et élastique, qui suscite un niveau d'effort élevé, tant réel que latent, une forte dépendance des pêches à l'égard des classes annuelles et de graves problèmes pour maintenir les taux d'exploitation à un niveau raisonnable.

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In an early review of stock and recruitment processes in exploited invertebrates, Hancock (1973) referred to the general lack of convincing information on the form of the stock–recruitment relationship in crustaceans. A decade or so later, we still have relatively few quantitative relationships to show between stock size and subsequent recruitment, despite an ever increasing pace of research.

This is in part due to the difficulties of defining unit stocks, due to problems in the age determination necessary for estimating appropriate lag times, but also because interspecific interactions and environmental effects contribute to the high variance around plots of recruits on spawners. Particularly for lobsters taken by passive gear, difficulties are also caused by seasonal changes in availability caused by migration, moulting and mating, and by environment effects on catchability, which in combination means that stock size estimates are rarely better than indices of abundance. For penaeid shrimps, for example, where ageing problems are minimized for essentially annual life cycles, Garcia (1983) has been unable to find unambiguous evidence for a stock–recruitment relationship. Here, autocorrelation between consecutive year-class strengths determined by long-term environmental fluctuations may lead to "spurious" stock–recruitment relationships.

Despite these apparently negative results, a large body of information has been accumulating on the impact of a wide variety of biotic and abiotic factors on crustacean recruitment, and alternative approaches to evaluating the effects of harvesting on population replenishment have been developed that seem to transcend the simple two-variable stock–recruitment models. These promise to lead to models based more soundly on the biology of exploited crustaceans, and this paper attempts to focus on the more promising of these.

## Alternative Approaches to Modelling and Assessment of Crustacean Stocks

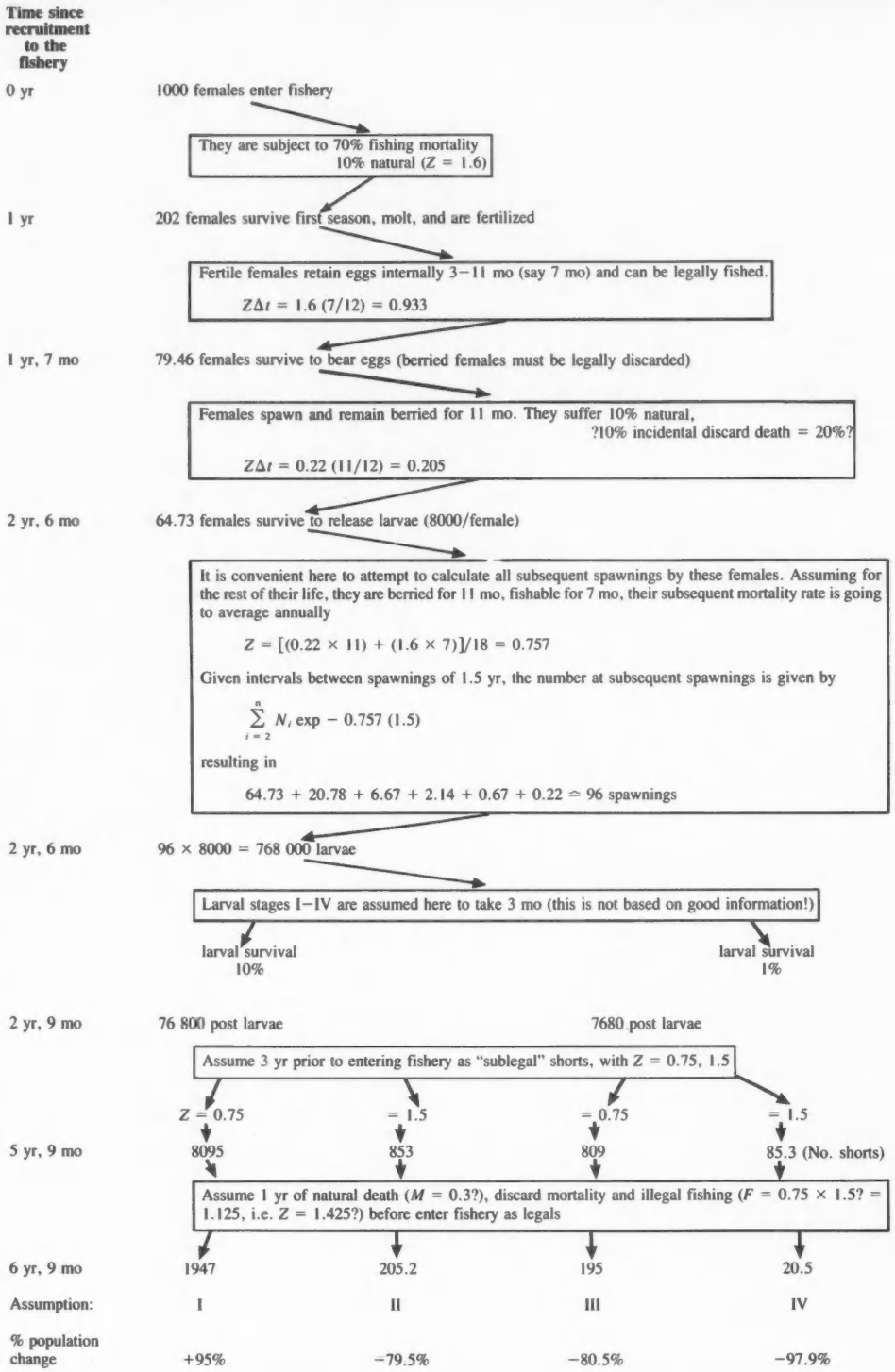
Considerable progress has been made over the last two decades (e.g. Hancock and Edwards 1967; Cooper and Uzmann 1971; Conan 1975; Conan and Gundersen 1979) in applying the yield per recruit modelling approaches of Beverton and Holt (1957) to crustaceans resources, even though these methodologies were developed for finfish stocks where continuous growth functions such as the von Bertalanffy can be reasonably assumed. It soon becomes evident in practice, however, that modelling growth-related processes in large crustaceans requires separate estimation of moult increment and frequency (Ennis 1978; Campbell 1983). Thus, although von Bertalanffy growth curves can be reconstructed, this approach has a distinct lack of flexibility; especially as for heavily exploited stocks, estimation of changes in reproductive potential is necessary.

### Cross-scheduling of Growth and Maturity in Crustaceans

Studies of crustacean physiology and behaviour (e.g. Aiken 1980) reveal a close linkage between scheduling of moulting and maturity, mating and egg laying, and this necessitates a brief examination of discrete growth models before reviewing reproductive processes in more detail.

The importance of estimating size at first maturity in crustaceans has been emphasized by fishery workers, but there are serious problems for large crustaceans in defining age at first maturity. Where the number of moults per year is a small but variable number at a given size, modal analysis could give anomalous results (Caddy 1977) if total number of moults at age (itself a function of past physiological factors and individual genetic makeup) is not constant. It may even be more reasonable to assume an arbitrary age at either entry to the fishery (Caddy 1977) or at maturity, and relate subsequent calculations to this benchmark, than to attempt the very difficult task of reconstructing moult scheduling prior to these events.

Some segregation at size may occur upon onset of sexual maturity in crustaceans (e.g. Campbell and Stasko 1985) and


Time since recruitment to the fishery
0 yr
1000 females enter fishery
They are subject to 70% fishing mortality
10% natural (Z = 1.6)
1 yr
202 females survive first season, molt, and are fertilized
Fertile females retain eggs internally 3−11 mo (say 7 mo) and can be legally fished.
ZΔt = 1.6 (7/12) = 0.933
1 yr, 7 mo
79.46 females survive to bear eggs (berried females must be legally discarded)
Females spawn and remain berried for 11 mo. They suffer 10% natural,
?10% incidental discard death = 20%?
ZΔt = 0.22 (11/12) = 0.205
2 yr, 6 mo
64.73 females survive to release larvae (8000/female)
It is convenient here to attempt to calculate all subsequent spawnings by these females. Assuming for the rest of their life, they are berried for 11 mo, fishable for 7 mo, their subsequent mortality rate is going to average annually
Z = [(0.22 × 11) + (1.6 × 7)]/18 = 0.757
Given intervals between spawnings of 1.5 yr, the number at subsequent spawnings is given by
$\sum_{i=2}^{n} N_i \exp - 0.757\ (1.5)$
resulting in
64.73 + 20.78 + 6.67 + 2.14 + 0.67 + 0.22 ≏ 96 spawnings
2 yr, 6 mo
96 × 8000 = 768 000 larvae
Larval stages I−IV are assumed here to take 3 mo (this is not based on good information!)
larval survival 10%
larval survival 1%
2 yr, 9 mo
76 800 post larvae
7680 post larvae
Assume 3 yr prior to entering fishery as "sublegal" shorts, with Z = 0.75, 1.5
Z = 0.75
= 1.5
= 0.75
= 1.5
5 yr, 9 mo
8095
853
809
85.3 (No. shorts)
Assume 1 yr of natural death (M = 0.3?), discard mortality and illegal fishing (F = 0.75 × 1.5? = 1.125, i.e. Z = 1.425?) before enter fishery as legals
6 yr, 9 mo
1947
205.2
195
20.5
Assumption:
I
II
III
IV
% population change
+95%
−79.5%
−80.5%
−97.9%

Footnote: This calculation does not allow for changes in fecundity/survival of large females or for multiple extrusions following mating.

FIG. 1. Hypothetical lobster life table beginning with entry of 1000 immature females into the fishery.

seems also evident for the Chilean squat lobster *Plueroncodes monodon* based on the work of Bustos et al. 1982. For this species, immature and mature population components migrate differentially at different depths and there is also some spatial segregation by sex.

It is obviously vital in sampling crustacean populations to know where and when spatial segregation by size and maturity occurs, and that the population is correctly defined and samples properly weighted by area before pooling and analyzing them for mortality rates using mean size statistics (Phillips et al. 1980), catch curve analysis (e.g. Caddy 1977; Pauly 1984), or cohort analysis using size frequencies (e.g. Jones 1984).

### Fecundity per Recruit Calculations

Modelling growth as a discontinuous process was suggested by Hiatt (1948) and further developed by Kurata (1956) and Mauchline (1976, 1977). Separate estimates of moult frequency and increment at size (the increment–frequency approach) avoids the redundancy of fitting a continuous growth model. More importantly it allows cross-scheduling of calculations of yield per recruit and fecundity per recruit (Caddy 1977, 1979a; Campbell and Robinson 1983), using simple Ricker or Thompson and Bell approaches (Ricker 1975) calculated over (changing) intermoult intervals, $\Delta t_i$.

Thus, although closed seasons and bans on landing berried females complicate the calculations, the total yield from $R = N_1$ recruits entering the fishery is assigned an arbitrary moult number $i = 1$, and yield from all moult classes up to a maximum number of moults ($N$) since recruitment is given by

$$(1) \quad Y_T = \sum_{i=1}^{N} N_i E_i (1 - \exp(-Z_i \Delta t_i)) \bar{w}_i$$

where $E_i$ is the exploitation ratio, $\bar{w}$ is the mean weight, and $Z_i$ is the total (annual) mortality rate, all for moult group $i$. The number surviving moult interval $i$ is then

$$(2) \quad N_{i+1} = N_i \exp(-Z_i \Delta t_i).$$

The calculation of population fecundity may also be somewhat complicated, depending on when spawning occurs in the intermoult period (assuming for simplicity here that the intermoult must be survived for an individual to contribute to population fecundity). Summing egg production by moult group, following entry to an arbitrary group $g$ (just preceding onset of maturity), gives total fecundity of all moult groups per $R'$ recruits since the start of group $g$ as

$$(3) \quad E = \sum_{i=g}^{N} R' P_i \exp(-Z_i \Delta t_i) \bar{e}_i$$

where $N_i$ is the number of females entering moult group $i$ (defined by Equation 2), $P_i$ is the proportion mature and spawning by the end of the interval, $Z_i$ is the total mortality rate (which can equal $M$ if that group is unfished), and $\bar{e}_i$ is the mean number of eggs spawned per female (this may represent more than two extrusions per intermoult in some species, e.g. Aiken and Waddy 1980).

## Conventional Stock–Recruitment Models as Applied to Crustaceans

### Construction of Life Tables as a Guide to Research Priorities

The use of life tables to describe the biometrics and demographics of a population has diffuse origins; it has most frequently been used in entomology and parasitology. A life table (e.g. Fig. 1) is referred to here in the quantitative sense of the relative numbers surviving to each of a series of critical stage in the life cycle, beginning at some arbitrary stage (usually the time of spawning or settlement), and ending at the same stage one generation later. By convention, the life table is usually calculated for the females in a population, reflecting in part the uncertainty that surrounds the effects of relative and absolute abundance of males and females to the recruitment process. This is a particular problem for crustaceans, where sex ratios may vary significantly from 1:1 due to either differential growth and availability or active selection by the fishery, and where the impact of sex ratios diverging from this ratio on reproductive success is poorly understood. Numbers present at each life history (or moult) stage and their corresponding survival rates at population equilibrium should result in one female being produced by the reproductive activities of one female a generation earlier, i.e. for females:

$$(4) \quad (R/S) \exp - \sum_{i=1}^{n} Z_i \Delta t_i = 1$$

at equilibrium, where $R$ = recruit numbers and $S$ = number of spawning females, each with $n$ stages in the life history suffering mortality $Z_i$ of duration $\Delta t_i$. This approach is somewhat complicated for multiple spawners, but this can be partly allowed for.

More critical can be density-dependent effects such as decreases in age at maturity, or changes in fecundity, that for some species (MacCall, pers. comm.) may compensate for changes in abundance such as caused by harvesting. In my opinion, it will be necessary to attempt to elucidate features of the fairly complex life history/fishery found in most decapod Crustacea before such density-dependent effects can be measured or taken into account. The fact that these factors are important seems, however, to be suggested by the relatively high resistance shown by some crustacean fisheries subject to recruitment overfishing.

For multi-age, multi-spawning species, modifications to the simple linear scheme described above can be (more or less successfully) incorporated to take account of the different options available to individuals as a result of differential growth, reproductive condition, and mortality schedules. An example shown in Fig. 1 based on Caddy (1978) uses mortality rates that are largely hypothetical, but based on some early ideas for the southwestern Nova Scotian lobster fishery, and resemble the approach of D. G. Robinson (pers. comm.). More recent work will have changed certain estimates, and this is merely intended to show that the constraint represented by Equation 4 allows relative orders of magnitudes to be placed on rates where one or two unknowns exist, if the population is to remain stable. It also clarifies the need to define survival rates such as those for discards, egg loss from berried females, etc., which are probably measurable, in order to be able to assist in estimating the more difficult to determine survival rates, such as in the early prerecruit stages. The limitations of this approach lead to the more complex probabilistic models touched on in a later section.

### Unit Stocks, Spawner–Recruit Models, and Crustacea

The identification of unit stocks, e.g. by statistical analysis of time trends of landings along the coast (see Campbell and Mohn 1983), but more directly by survey for species showing

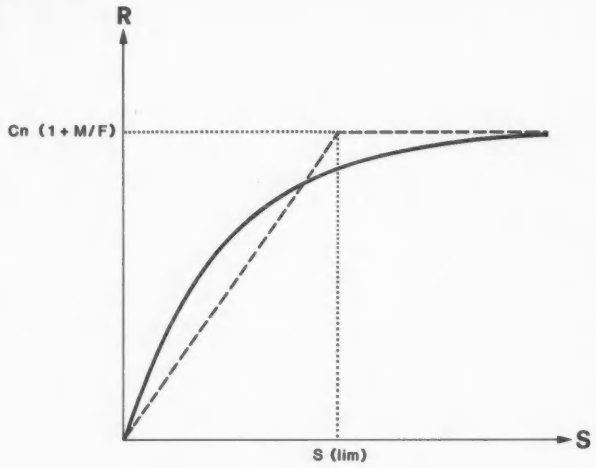



FIG. 2. Beverton and Holt type of stock–recruitment relationship, and a simple ramp function approximation.

spawning or nursery areas, is a necessary precondition for stock–recruitment studies and provides the best indications of possible stock structure. (Needless to say, investigation of stock–recruitment relationships without prior stock definition is a waste of time.)

The possible application of conventional stock–recruitment relationships such as the dome-shaped Ricker (1954) and the asymptotic Beverton and Holt (1957) models to Crustacea has been a subject of some discussion in the literature, and the general consensus seems to be that the latter type of model is a priori more likely to apply to crustaceans. The reasoning is that intraspecific competition between spawners and competition between spawners and recruits (e.g. cannibalism), which are factors generally held to be major causes of a dome-shaped stock–recruitment relationship, are unlikely to be major factors in decapod crustaceans, especially where juveniles and adults occupy different grounds. This conclusion may be premature given that cannibalism is a notable feature in juvenile lobsters held at high densities (e.g. Sastry and Zeitlin-Hale 1977) and observations by Chittleborough and Phillips (1979) which suggest that there may be density-dependent mortality on crowded nursery reefs for age 1–4 juveniles of western rock lobsters. (It may be noted that this finding seems to contradict the apparent value of puerulus collectors for fishery forecasting.) Morgan et al. (1982) also fitted a Ricker stock–recruitment curve to the relationship between spawning stock size and puerulus settlement 9 mo later. Chittleborough (1979) also suggested that female fecundity may be affected by high density.

Despite these latter studies, it may be worthwhile pursuing the concept of a Beverton and Holt density-dependent recruitment relationship between recruits ($R$) and spawners ($S$),

$$R = S/(A + BS),$$

a little further to see whether any of its features can be reconciled with those particular to a sedentary or semisedentary crustacean. Given the relationship between $C$, catch (in numbers) from a cohort in all years (harvesting complete), and the original recruitment $R$, and assuming that this relationship also applies under stable conditions to the sum of catches from all cohorts in one year, we can write for the asymptotic level of recruitment

$$(5) \quad C = RF/Z \text{ or } R = C(1 + M/F).$$

If we now assume that there are nursery areas for which mean prerecruit density $\bar{D}$ is known, then the effective area of grounds, $A_R$, producing recruits is given by

$$A_R = C(1 + M/qf)/\bar{D}.$$

If $M$ is the annual rate of natural mortality and $F$ is the annual fishing mortality (or as in the second formulation, the fishing effort $f$ times the catchability coefficient $q$), it seems worthwhile making this calculation for all periods of relatively constant exploitation in the fishery, especially in the early years of the fishery when recruitment was probably on the asymptotic plateau. It is interesting to look again at the original Beverton and Holt relationship, and consider that when the asymptote is reached,

$$BS \gg A$$

and therefore that

$$R \rightarrow 1/B = C(1 + M/F).$$

This should allow solution for parameter $B$ if the catches and the ratio $M/F$ are known during the early years of the fishery. Hence, it might also allow a solution for $A$, if spawning stock size or population fecundity and number of recruits are known for several pairs of years.

Garcia (1983) illustrated this asymptotic relationship for penaeid shrimp by a simple ramp function (Fig. 2) where above a given stock size, which we may refer to as $S$ (lim), recruitment is more or less constant. With recruitment defined as in Equation 5, it may be reasonable to try to roughly estimate $S$ (lim) by equating it to that stock size which, given an overall mortality rate $Z'$ during larval and juvenile life stages of duration $\Delta t$, produces just enough postlarvae that competition for space in larval settlement areas and/or juvenile rearing areas is minimized, i.e. where

$$S\,E \exp(-Z'\,\Delta t) \leq R.$$

## Relative Impacts of Physical Environment and Stock Size on Reproduction

In classical stock–recruitment models, and some of their refinements (e.g. Harris 1975; Shepherd 1982), all variables other than parent stock size are treated as "noise," and it may be questioned whether the search for a simple, two-parameter deterministic relationship between spawners (population–fecundity) and progeny recruiting to the fishery lag years later is realistic, given that for many crustacean fisheries we have more detailed information on factors underlying recruitment success, of which spawning stock size is only one of them, and possibly not the most important one. An interesting discussion of the pros and cons of the environment versus stock size debate that has arisen in recent years among penaeid shrimp biologists is given in Garcia (1983), which is referred to in the following brief discussion. Although most penaeids can be regarded as annual species, thus posing rather special stock–recruitment problems, the arguments are fundamentally similar to those discussed in the literature on larger reptant Crustacea with lifespans in excess of 1 yr.

On the one hand, we could take the view of Walters and

Ludwig (1981) that since spawning stock size is the only factor controlled by management, the fact that recruitment can be predicted more accurately from environmental variables than from spawning stock size is irrelevant (in fact, the extent of juvenile habitat may also be potentially controllable in some cases; see later). The danger that recruitment may be affected is an important cautionary consideration when spawning stock size is reduced, and a suggestion that this may have occurred for *Penaeus esculentus* following decimation of the spring spawning by unusually high levels of effort is made by Penn (pers. comm. in Garcia 1983).

The opposite view was expressed by Neal (1975) who was unable to identify any spawner–recruit relationship in Gulf of Mexico penaeid shrimp populations, and who suggested that this would almost inevitably be the case, given high individual fecundities and the flat-topped spawner–recruit curve described in Fig. 2.

Rainfall, temperature, river outflow, and area of estuarine habitat have all been suggested to exert more control on penaeid recruitment than parent stock size (Garcia and Le Reste 1981; Staples et al. 1981; and others cited in Garcia 1983). This last author noted that statistical correlations observed between recruitment in successive years are quite likely to have resulted from strong serial autocorrelation of apparent abundance data (acting through estimates based on catch-per-unit effort and fishing effort) through environmental forcing of recruitment. This can lead to apparently linear stock–recruitment relationships that should properly be regarded as artifacts. In his opinion, the existence of stock–recruitment relationships in penaeid shrimp still remains to be demonstrated; at the very least, a family of stock–recruitment curves of the Beverton and Holt type are postulated, with potentially different parameters occurring each year depending on environmental conditions (or even in the case of multiple spawners, for each month). Looking in more detail at the question of spawner–recruit relationships for an annual species with a series of seasonal cohorts, Garcia (1985) stressed the fact that selective depletion of the main monthly cohorts by aimed shrimp fisheries reduces potential reproductive output by introducing a mismatch between the most favourable timing for the reproductive cycle and the effective timing of the fecundity cycle for the survivors of exploitation.

Considering now the generally longer-lived Macrura and Brachyura, similar conclusions seem evident to those expressed above for penaeid shrimp. The importance of environmental variables is attested to by simple correlations of catch and environmental variables from the early studies summarized in Dow (1977) on the relationship of environmental temperature trends in commercial catch of American and European lobsters. Flowers and Saila (1972) for the Gulf of Maine inshore lobster fishery showed that with surplus effort, yield must be largely dependent on recruitment, so that yield predictions can be made using only lagged and present temperatures and the key recruitment control variables. This conclusion set the scene for the development of delayed recruitment models by Marchessault et al. (1976) in which a delayed recruitment function is incorporated into a production model which presupposes some positive relationship between parent stock and recruitment. The success of more recent Box-Jenkins types of models in predicting yield is an index of their future promise (see Fogarty and Murawksi 1984) or production modelling approaches that use total mortality ($Z$) rather than fishing effort as the control variable (Csirke and Caddy 1983).

Variables other than temperature have been postulated to be of importance to crustacean recruitment, e.g. between river outflow and lobster catch (Sutcliffe 1973) in the Gulf of St. Lawrence, lag = 7 yr later (where 7 was believed to be the age at first recruitment at close to the northern limit for this species). This parallels similar relationships found for penaeid shrimp (reviewed in Garcia 1983) in various parts of the tropics. The importance of oceanic/atmospheric variables in producing periodicities in recruitment of California Dungeness crab is also suggested from the work of Methot and Botsford (1982), who commented that variations in recruitment success for Dungeness crab are even greater than the already pronounced fluctuations in annual landings. The importance of seasonal timing of larval release on subsequent survival of lobster larvae is illustrated by the analysis of Caddy (1979b) which seems to indicate that late-produced stage I larvae in the southern Gulf of St. Lawrence have a limited chance of survival in most years. They may be "insurance" against the occurrence of extreme climatic conditions for a benthic species where surface water conditions of relevance to larval survival cannot be predicted from bottom temperatures, especially where stratification typically occurs. Relating abundance of stage IV larvae to subsequent recruitment into the fishery is far less simple, and as noted by Scarratt (1973), recruitment of a given cohort may be spread over several years, obscuring any obvious relationship, an observation made earlier in relation to modal analysis. This potentially mixed-age population of recruits would seem a priori to be a factor obscuring any simple stock–recruitment relationship. It should not, however, discourage attempts to apply relative abundance versions of the stock–recruitment models to explore, for example, the relationship between abundance of sublegal small lobsters ("shorts") and mature lobsters a biologically meaningful period of years previously.

## Approaches to Stochastic Modelling of Crustacean Populations

As we have noted, the discontinuous growth patterns characteristic of crustaceans can be modelled by a continuous growth function, but there seems to be little advantage in ignoring the moult cycle, given that related functions such as moult frequency and fecundity are more easily related to size than to age. Age is particularly difficult to determine in the wild for decapod crustacean populations, given that scheduling rather complex and conflicting events such as moulting, egg fertilization, and often prolonged periods of egg-holding on the female are important questions economically, and are not easily dealt with using continuous growth functions, and in fact have an impact on the form of the growth curve (e.g. Fig. 3).

In relation to yield modelling of populations of the American lobster, *Homarus americanus*, deterministic versions of a yield per recruit and fecundity per recruit calculations were referred to earlier, which use length-related inputs for moult increment, moult frequency, and maturity/fecundity, all of which are feasibly obtained from field and laboratory experiments. One of the limitations of this simple modelling approach is that it does not allow a proper representation of some of the more complex "choices" that an individual (female) lobster faces in the course of its life. A normal stochastic formulation in which a probability is associated with each "choice" (e.g. to moult or not to moult, to enter a trap or not, etc.) does not easily take into account vital information on the "state" of an individual animal

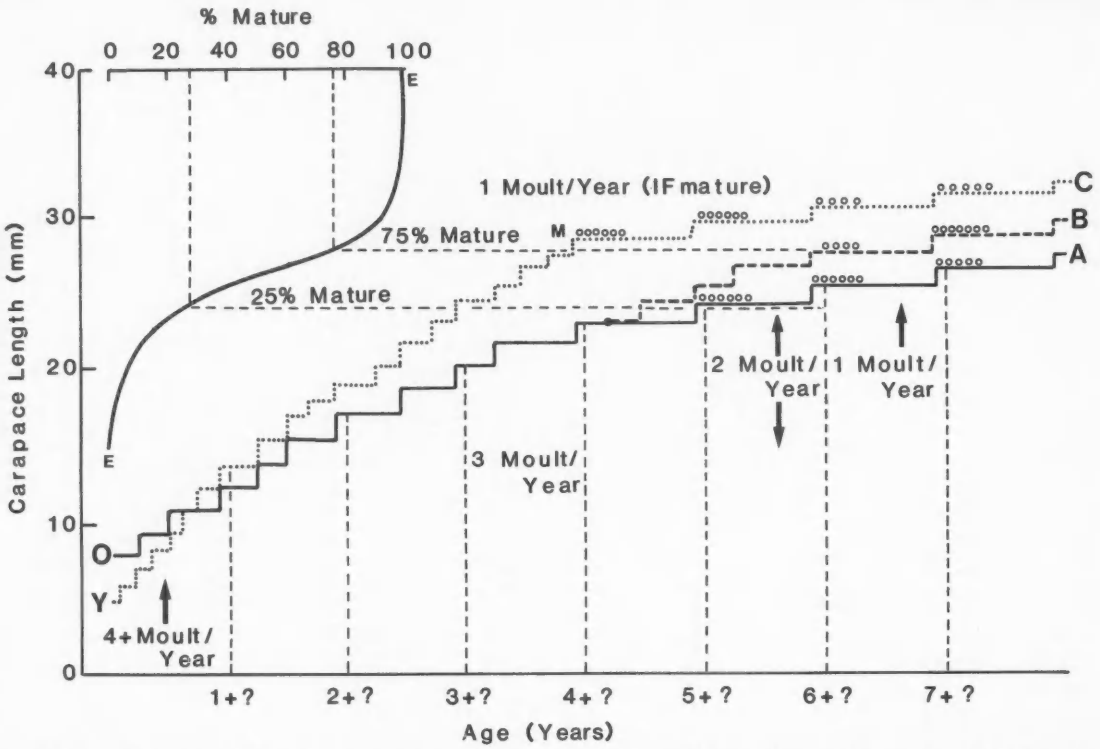



FIG. 3. Possible impacts of differential size at maturity on form of growth curve for the squat lobster, *Pleuroncodes monodon*, given information in Bustos et al. (1982). Discontinuous growth curves $O-A$ and $O-B$ following the number of molts per year suggested in Bustos et al. (1982) assuming onset of maturity at 25 and 75% of the population, respectively. Curve $Y-C$ is fitted assuming a larger number than three molts in the first year and onset of maturity at 75% of the population mean.

of a given size at a given time of year, such as, for example, when it last moulted, mated, or extruded eggs, or whether it has stored spermatheca, etc., all of which are relevant to its further "decisions" in the model. One approach that seems promising here resembles the theory of Markov chains, a probability structure which seems a good starting point for modelling a series of dichotomies in the course of the life history (Fig. 4). Although the sum of probabilities of any individual ending up in an absorbing state (captured, death in discarding, death from natural causes) equals 1 (Olinick 1978), a great number of events can occur in the "decision tree" preceding these "end points." Such transition probabilities may not be known for each intersection in the decision tree, but such a decision tree model, incorporating "best guess" values, should be of great utility for sensitivity analyses and in planning research priorities, even if the assumptions for Markov processes (e.g. that these probabilities are independent of past states) are not exactly met.

There are at least two fundamental difficulties in attempting to represent a detailed sequence of biological and fishery-related events in the life history of a commercially exploited decapod by the usual cohort models.

The first is the problem of defining the time units. Many crustacean fisheries (particularly trap fisheries) are faced by strong seasonal fluctuations, which affect availability and catchability. These fluctuations depend on a seasonality which may be reflected in changing water temperature or weather conditions. Without going into details on the environmental variable concerned, input of this unspecified seasonal forcing variable may be represented by a sine function, for example, whose periodicity is 1 yr and whose amplitude is variable, depending on whether a strong or weak seasonal effect is looked for. Temperature is likely to be the main driving function in high latitudes, and population measures such as moult frequency (McLeese and Wilder 1958) and catchability (Paloheimo 1963) can also be considered to be simple functions of temperature.

It seems convenient, then, to consider two time scales in such a model: the first, real time, the second, physiological time. This second variable may be considered to be made up of units, each unit being the (variable) period of real time needed to complete a given physiological function, such as, in this case, a cycle of ecdysis. In northern latitudes a unit of physiological time would thus correspond to more units of real time in winter than summer. From a modelling perspective, this would mean that intermoult periods, time from fertilization to egg extrusion, and time to hatching could be modelled as quantities occupying a constant number of units of physiological time. These could subsequently be converted to real time, perhaps using an underlying sine function to convert from physiological to real time units, $t$, e.g. $t = a \cdot \sin(t' - T)$, where $T$ = the periodicity of the cycle (1 yr) and $t'$ is the number of units of physiological time involved. Adjustments would have to be made also for size and state of maturity, presence of external eggs, etc.

Although moulting processes seem to lend themselves to

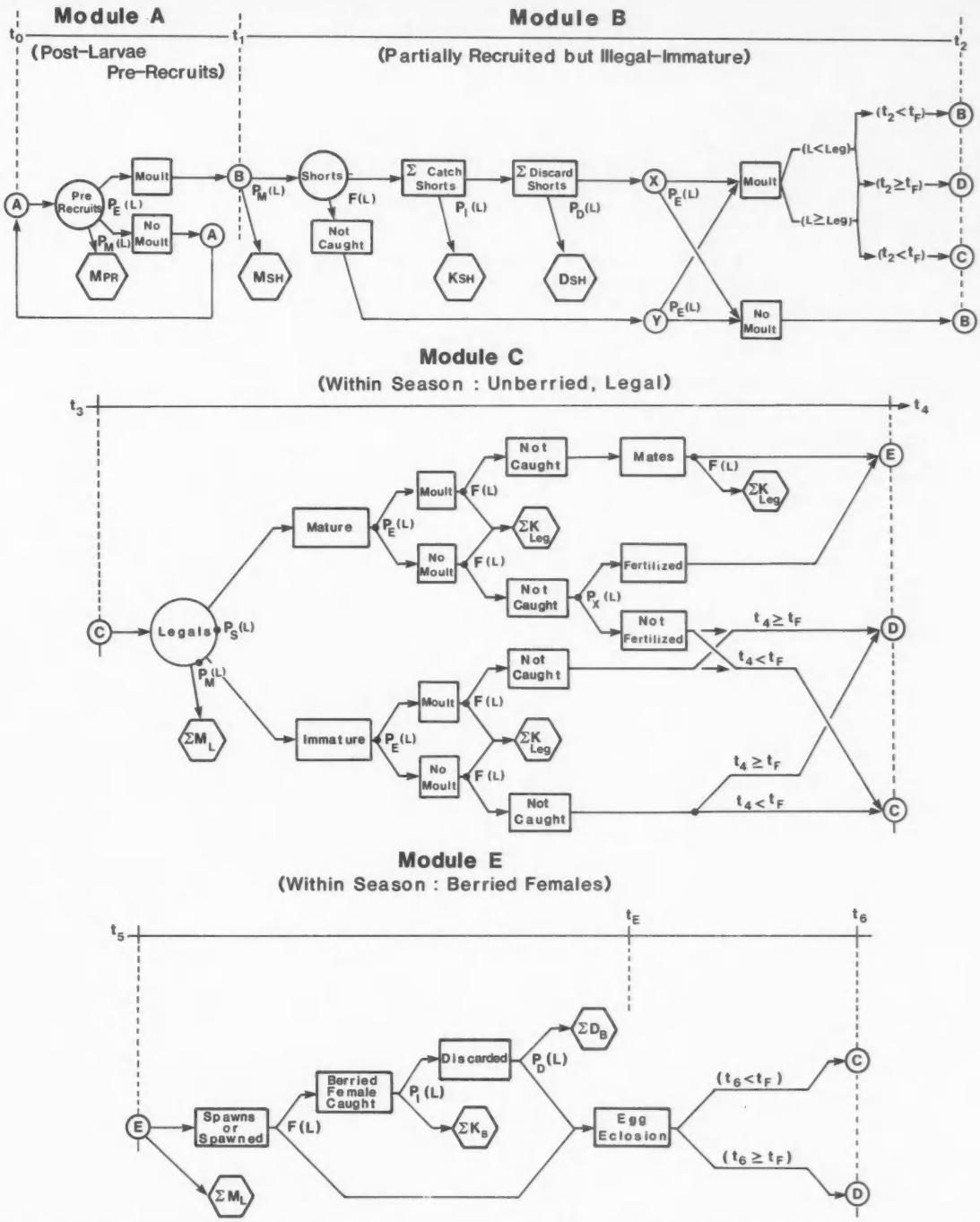



FIG. 4. Modules for a probabilistic harvesting model for lobsters. $D_B$ = sum of deaths of berried lobsters in discard; $D_{SH}$ = sum of deaths of sublegal lobsters ("shorts") in discard; $F(L)$ = size-specific fishing mortality; $K_B$ = sum of "scrubbed" berried females retained illegally; $K_{LEG}$ = sum of legal lobsters retained; $K_{SH}$ = sum of "shorts" illegally retained; LEG = legal minimum size; $M_L$ = sum of natural deaths (legals); $M_{PR}$ = sum of natural deaths (prerecruits); $M_{SH}$ = sum of natural deaths (shorts); $P_D^{(l)}$ = probability of dying in discard (function of length); $P_E^{(l)}$ = probability of ecdysis (function of length); $P_I^{(l)}$ = probability of illegal retention (function of length); $P_M^{(l)}$ = probability of natural deaths (function of length); $P_S^{(l)}$ = probability of maturity (function of length); $P_X^{(l)}$ = probability of being fertile (function of length); $t_s$ = start of fishing season; $t_f$ = end of season; $t_E$ = time eclosion.

modelling in physiological time (as might also, for example, change in activity and catchability with temperature for a species showing active attraction to the trap, e.g. Paloheimo 1963), this scale does not accommodate itself easily to the harvesting sector of a model, e.g. events such as the onset and end of fishing seasons. The most feasible modelling approach here may be to convert the basic units of physiological time in which the biological components of the model are expressed into real time, accumulate these on a counter, and decide when a given physiological event or module is complete in real time.

Hierarchy of Choices

The time interval(s) used in such a model are conveniently considered both on an annual basis and over some small time interval (e.g. weekly, fortnightly, monthly). Within these smaller time intervals, each individual encounters a series of choices which can be expressed in hierarchical form as follows:

| Hierarchy | Choice |
|---|---|
| I | Dies naturally in interval/Does not die naturally |
| II | Moults/Does not moult |
| (E) | Captured/Not captured<br>Discarded/Retained<br>Survives discarding/Dies incidentally |
| III | Fertilized/Not fertilized (immature?) (eliminate for males) |
| (E) | As above |
| IV | Extrudes eggs/Does not extrude eggs (eliminate for males) |
| (E) | As above |
| V | Releases larvae/Does not release larvae (eliminate for males) |
| (E) | As above |

The intention in the above tentative scheme is that the "physiological choices" be modelled as far as possible in physiological time units and the fishery-related processes (modules E) in real time, mortality rates being adjusted from real elapsed time. Given that we are discussing here the desirability of developing a model which can take into account most important details of the biology as well as the fishery, but will need to be modified in the light of circumstances, some modules for such a model are given in Fig. 4. Such a model is unlikely to be fully realistic at an early stage, but it would be a useful exercise towards elucidating some of the key questions (here posed as probabilities and unknowns) for the species in question.

## Niche Availability and "Bottlenecks" in Crustacean Recruitment

Although planktonic stages of crustaceans can sometimes be long, by contrast, settlement and prerecruit areas may be rather specific, both for palinurids (e.g. Chittleborough and Phillips 1979; Morgan et al. 1982) and for penaeid shrimp (e.g. FAO/UNDP 1983), and a number of investigations have approached the difficult problem of characterizing factors that may limit prerecruit production in these areas. This necessarily involves better definition of the ecological niche occupied by prerecruits, and this is of prime importance for stock enhancement work also.

Recognizing that most benthic Crustacea pass through a cryptic stage following settlement, a potentially valuable mathematical tool for investigating the size spectrum and abundance of the crevices or "niches" (in the purely physical sense of the term) is provided by the concept of the fractal dimension of a given habitat (Mandelbrot 1977), a concept that is finding wide application in terrestrial arthropod studies (e.g. Morse et al. 1985). Although active burrowing can directly affect the number of "crevices" available on soft bottoms, for those species dependent on marine vegetation, coarse sediments, or outcroppings/coral reefs during critical postlarval stages, this concept may provide a method of identifying any possible "bottlenecks" in the recruitment process.

The ecological niche as a seminal concept in marine ecology has experienced progress from its original form, describing the physical "concavity" serving as shelter (from predation) for the species to the all-embracing Hutchinsonian interpretation of a niche, defined by Kerr and Ryder (1977) as "that abstract hypervolume that is generated by assigning a dimension to each factor affecting an organism's survival." With the development of the concept of the fractal surface (Mandlebrot 1977), there is an argument for at least some purposes, for returning to a more limited three-dimensional interpretation of the "niche" as "that unit of bounded space which when occupied by an individual organism, improves that organism's chance of survival." This definition has the advantage of leading more directly to an experimental approach, particularly for recruitment studies of organisms such as lobsters and reef fish that are obligate crevice dwellers for part or all of their lives. Indications that recruitment and subsequently mortality processes are crevice limited for some coral reef fish have been alluded to by several authors (e.g. Lavett-Smith 1975) and undoubtedly has application for benthic crustaceans also.

The idea of modelling recruitment–mortality processes as a function of niche availability, rather than as dependent solely on intrinsic factors such as size and age of organism, has rarely been expressed quantitatively, probably because it is assumed that the size spectrum of physical niches is not readily available to measurement. This is true in many cases, but it seems likely that certain indirect measures of niche availability with size can be found.

Our knowledge of the geometry of natural surfaces (Appendix) suggests that an obligate crevice dweller for all or part of its life history will usually be faced with a decline in number of niches or crevices as it grows, and the available size spectrum of crevices will impose certain life history constraints, which in the long run will have an impact at the evolutionary level.

The organism then faces three alternatives: (1) migrate to another locality, (2) if growth is habitat independent, compete for a declining number of larger crevices, and suffer a high risk of predation if unsuccessful, or (3) slow or stop the growth rate (by stunting) until a larger crevice becomes available.

The relevance of long migratory movements to the stock–recruitment process in many lobsters and the behavioural adaptations that may accompany them (e.g. see Herrnkind 1977) seems to be related to reproduction, in that areas of spawning may correspond hydrographically to situations which result in high return rates of larvae to favourable nursery areas (see Booth 1979). The possible influence of lack of niche availability at size in initiating migratory movements seems not to have been considered.

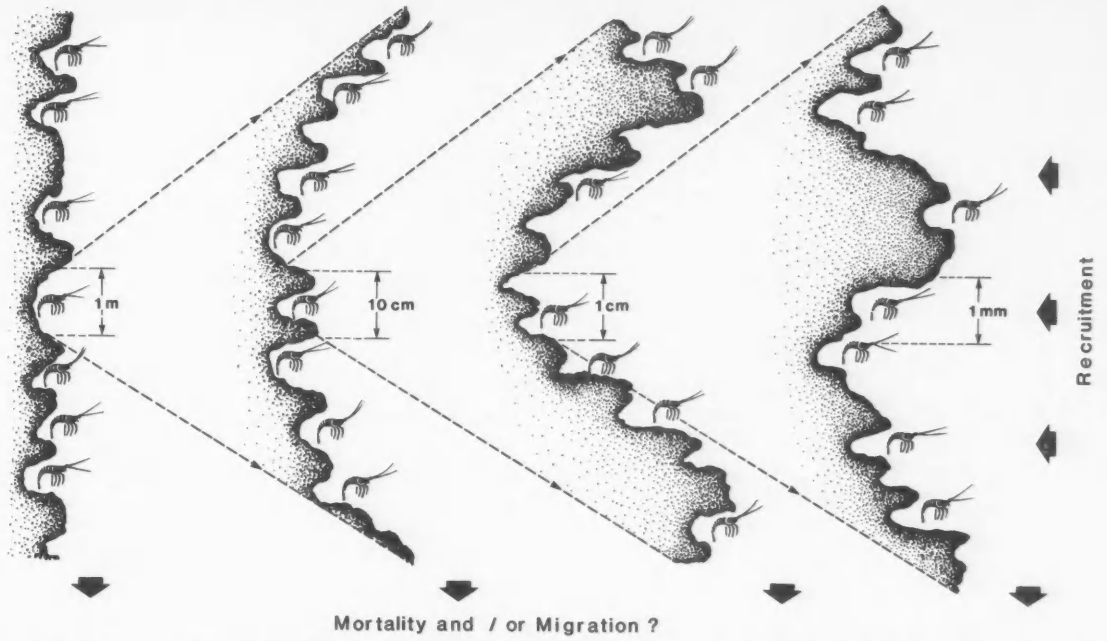



FIG. 5. Progressive scales of magnification of a fractal surface (right to left) and how a crevice-dwelling organism such as a lobster would face continual reduction in the number of physical niches available to them as they increase in size.

The Appendix develops a tentative framework for considering the implications of a fractal surface, particularly for survival and recruitment of crevice-dwelling species such as young lobsters. Recruitment processes may be considered to be a special case of queueing theory, or what can conveniently be referred to as the "musical chairs" model of mortality processes in recruitment (Fig. 5).

Several authors have noted that natural substrates are unlikely to be simple fractals throughout their size spectrum, but it may be precisely such "discontinuities" that are important for recruitment processes. Figure 6 shows the predicted form of the number of niches with size, assuming the natural surface is a fractal with two values of $D$ from 2.05 and 2.79. This figure illustrates two possible applications: assuming hypothetically in the case of line $Y - B - B_1$, that the natural surface shows a change in its fractal characteristics at around 3 mm (point $B$), this might contribute to a bottleneck in postlarval survival, in that number of crevices subsequently falls off more rapidly with size than previously; in the case $Y - A - A_1$, the opposite effect is postulated, possibly as a result of habitat enhancement increasing the effective number of crevices.

Figure 7 shows the predicted natural mortality rate with size from Appendix Equation 5, assuming two values of $D$, and values of von Bertalanffy parameters in the not-unreasonable range for *H. americanus* of $L_\infty$ (total length) = 40 cm, $K$ = 0.15, and $t_0 = -0.5$. The predicted value of $M$ (which goes up sharply with $K$) is high for small individuals, but drops off to low values in the commercial size ranges, at and below those of $M = 0.1$ accepted as reasonable for this species.[1]

[1]It is interesting to speculate also on the effect of available niche size spectrum on $L_\infty$ for homarid lobsters: is the large maximum size of offshore H. *americanus* a function of availability of large shelters in submarine canyons and terminal morraines?

Higher natural mortalities are predicted by the above equation for surfaces with a higher fractal value, and these also fall off more rapidly with size, but higher $M$'s occur with increases in the value of $K$. (We may question whether relatively low values of $K$ are not an evolutionary advantage to large crevice-dwelling organisms). This effect produces, from a different theoretical base, the type of trajectory for $M$ predicted by Cushing (1975) for natural mortality of plaice, namely a rapid decline in $M$ with age to a slowly decreasing, more or less constant value. From a yield per recruit point of view, it would be likely to lead to relatively constant production, irrespective of a reasonable range of $F$, especially if growth rates are density dependent.

## Experimental Approaches and Practical Implications

The difficulty of measuring the fractal dimension of a substrate has been alluded to, and one possibility, namely measuring the size spectrum of all crevice dwellers by some procedure analogous to rotenone sampling, seems feasible. Another experimental alternative suggests itself, namely placing artificial substrates in the nursery area, each perforated with a fixed number of randomly placed holes of known dimension over a range of discrete sizes. If these prove suitable for colonization, it is reasonable to suppose that the proportion occupied under equilibrium at a given size will be a function of the occupancy rate of naturally occurring holes of the same size in nature, but more easily measured. Any bottlenecks in the growth/recruitment process would then presumably show up as peaks in the plot of proportion of occupied holes at size.

The limiting influence of juvenile survival on fishery production is hinted at by certain behavioural patterns in the immature stages, such as clumping of juvenile rock lobsters (Berrill 1976) and the formation of "balls" of juvenile king crabs. The

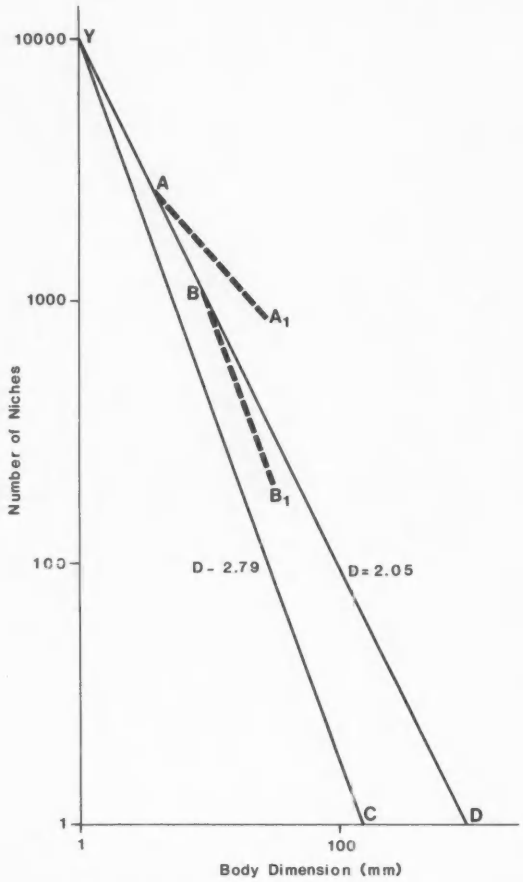



FIG. 6. Logarithmic function of predicted number of physical niches with size (linear dimension) for two values of the fractal coefficient, *D*.

significance of these special behavioural adaptations at least hints at the need for a mechanism to increase survival rates of stages particularly vulnerable to predation. The question that might be considered is whether at low densities this type of behavioural mechanism still can function, and if not, what is the impact of low density on individual survival.

## Interspecific Effects on Crustacean Recruitment: Predation and Competition

In addition to intraspecific and environmental factors, and the possibility of habitat limitation at critical stages, an important and often overriding factor on recruitment can be predation or competition for habitats.

Pauly (1980) suggested for Gulf of Thailand shrimp stocks occurring in a mixed trawl fishery that annual recruitment is related to annual egg production ($P$) and to the biomass of predators and competitors ($B$) in a highly diverse community of bottom organisms harvested by a multispecies trawl fishery. He derived for this situation the relationship

$$\log_{10}R = 3.440 + 1.26 \log_{10}P - 0.6708 \log_{10}B.$$

Similar relationships may be developed for other crustacean fisheries, where the crustacean is a component of a trophic triangle (Ursin 1982), especially if this contains other exploited species or organisms liable to stock fluctuations.

Examples in the literature where relative abundance of predators may be of at least equal importance to parental stock size in determining recruitment are snow crabs (Bailey 1981), pandalid shrimp (Lilly 1984), and king crabs (Incze et al. 1986).

The competitive relationship postulated between species sharing the same habitat, e.g. offshore lobsters and other members of the "pueblo" community, including Jonah crabs, described for offshore canyons (Cooper and Uzmann 1971, 1977), could also provide intraspecific constraints on recruitment determined by the number of burrows or crevices available in the same way as this has been postulated for reef fish (e.g. Lavett-Smith 1975).

In a variety of other situations, habitat limitations may be confounded with intraspecific associations, such as where some other organism provides critical habitat. Thus, Price (1982) noted that seagrass beds seem to be a preferred habitat for juvenile *Penaeus semisulcatus* in the Gulf, and this relationship between fauna and epiflora also appears to apply to other crustaceans. The relationship between *H. americanus* in southern Nova Scotia and *Laminaria* (a favoured habitat for lobsters) has been postulated to be mediated through the browsing behaviour of sea urchins, a prey of lobsters. This has been discussed by Pringle et al. 1982, and the details of this ecological interrelationship are still being investigated. Similar relationships apply for palinurids, where eel grass beds or nursery reefs may play a key role in the life history. Since the effects of human activities will often be to result in a loss of cover (epifauna and epiflora) that may be needed by critical stages, care should be taken to identify these possible effects before accepting a misleading statistical relationship between other variables, e.g. between recruits and adult stock size and/or hydrographic factors.

If nursery areas are limited and density dependence or competition occurs there, the delimitation of possible "bottlenecks" provides the best clue to stock enhancement possibilities, rather than the simple investigation of statistical artifacts of stock–recruitment.

## Summary and Conclusions

### General Considerations for Fitting Stock–Recruitment Models to High Value Crustaceans

It is significant that lobsters (homarids and palinurids), many crabs, and shrimp are high unit value resources. As a result the catch rate and population density that permits an economic return is lower than for low unit value resources. As noted by Panayotou (1982), in some circumstances, as in the case of a number of crustaceans such as lobsters, market demand has shown a high elasticity of prices. As a consequence, the fixed price function invoked in simple economic models could possibly be replaced by a price curve that slopes progressively upwards as overall catch declines and density decreases. This might explain the great difficulty experienced in trying to manage such resources at below MSY, and poses the question as to which management criteria it would be preferable to follow under these circumstances. More to the point in the present context, since fisheries under uncontrolled effort tend to move

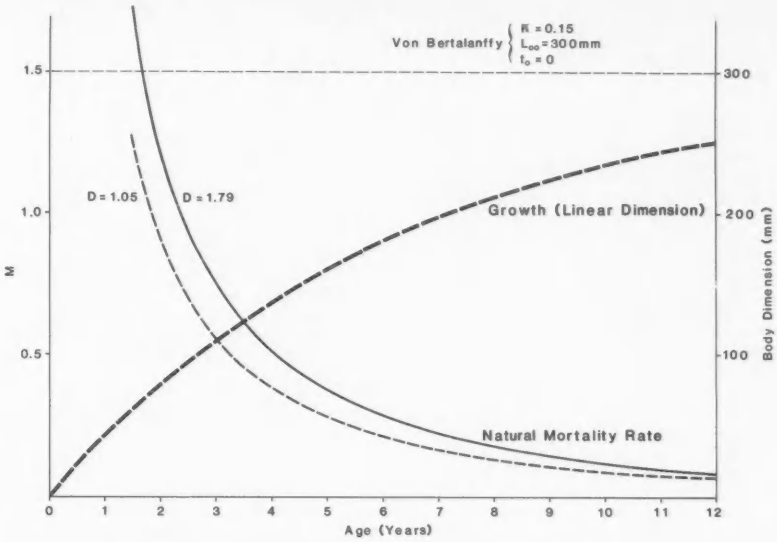



FIG. 7. Change in predicted natural mortality rate ($M$) with size and age for obligate crevice dwellers from Equation A.5, von Bertalanffy growth coefficients typical of *H. americanus*, and two fractal coefficients, $D$.

to the point of zero rent at low stock size, we may expect to find for most developed crustacean fisheries that we are currently in the area where incoming recruitment plays a large part in the annual yield. We would expect then to be to the left of any point of inflexion in the spawner–recruit curve, if a dome-shaped model applied, and thus in a situation where understanding the factors affecting recruitment becomes of paramount importance.

As a consequence, many, if not most, high value crustacean resources are subject to exploitation rates that are at or beyond most of the conventional "bench marks" such as $f_{MSY}$ and $F_{max}$ suggested by the usual yield models, and are likely also to be at a stock size below the "locus of maximum surplus reproduction" (LMSR) of the Ricker spawner–recruit relationship, if this applies.

All of the above makes it difficult, if not impossible, to establish what is the stock–recruitment relationship for most crustaceans, especially those with a long history of exploitation, since the same considerations apply as were noted by, for example, Hilborn (1979) in relation to fitting production models, namely that we need data points that span the whole possible range of action of density-dependent effects before such a relationship can be derived with any degree of confidence (even assuming that biotic and abiotic effects remained constant). This may have one advantage. If, as seems likely, it proves difficult to manipulate stock density in an experimental management regime such as Hilborn suggested, given that we are likely to stay at low spawning stock sizes, there is no real difference between the two (dome shaped and asymptotic) formulations and we probably will not go too far wrong assuming a ramp function between stock and recruitment for low to moderate stock sizes.

## Combining Various Elements in a Model of Crustacean Stock–Recruitment

If, as suggested in this paper, recruitment of Crustacea can be expressed as a function not only of parental stock size, environment, predators, and competitors, but also of area of habitat available at some critical stage prior to recruitment, then estimating the number of recruits in year $t$ is likely to require a formulation containing the following terms:

$$Rt = f(S_{t\text{-LAG}}, A_{t\text{-LAG},t}, Bp_{t\text{-LAG},t}, E_{t\text{-LAG},t})$$

not necessarily in order of importance, where $S_{t\text{-LAG}}$ is the spawning stock size or fecundity (LAG = age at recruitment) years previously, $A_{t\text{-LAG},t}$ and $B_{t\text{-LAG},t}$ are, respectively, the critical areas of juvenile habitat and the relative density of predators or competitors, at some point in time between spawning and recruitment, and $E_{t\text{-LAG},t}$ is the value of any environmental variable which is known to affect spawning or recruitment success.

Defining the relative importance of these factors and the appropriate lag times has obvious implications for the programme of research involved.

## References


AIKEN, D. E. 1980. Molting and growth of lobsters, p. 91–163. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

AIKEN, D. E., AND S. L. WADDY. 1980. Reproductive biology of lobsters, p. 215–276. *In* J. S. Cobb and B. F. Phillips [ed.] Biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

BAILEY, R. 1981. Catch prediction for the snow crab (*Chionocetes opilio*) fishery in the Southwestern Gulf of St. Lawrence: a problem of predation by cod (*Gadus morhua* L.). CAFSAC Res. Doc. 8/11: 7 p.

BERRILL, M. 1976. Gregarious behaviour of juveniles of the spiny lobster, *Panulirus argus* (Crustacea: Decapoda). Bull. Mar. Sci. 25: 515–522.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. Lond. Ser. 2, 19: 533 p.

BOOTH, J. D. 1979. North Cape — A 'nursery area' for the packhorse rock lobster, *Jasus verreauxi* (Decapoda: Palinuridae). N.Z. J. Mar. Freshwater Res. 13(4): 521–528.

BRADBURY, R. H., R. E. REICHELT, AND D. G. GREEN. 1984. Fractals in ecology: methods and interpretation. Mar. Ecol. Prog. Ser. 14: 295–296.

BUSTOS, H. E., O. L. ATACENA, S. A. MORA, AND W. E. PALMA. 1982. Estudio de crecimiento y edad en el recurso largostino colorado (*Pleuroncodes monodon* H. Milne Edwards, 1837). Feb. 1982, Report of Instituto de Fomento Pesquero, Jose Domingo Canas 2277, Santiago, Chile. 120 p.

CADDY, J. F. 1977. Approaches to a simplified yield-per-recruit model for crustacea, with particular reference to the American lobster, *Homarus americanus*. Fish. Mar. Serv. MS Rep. 1445: 14 p.

1978. Preliminary calculations of population fecundity for SWNS and offshore lobsters. CAFSAC Working Doc. 78/4: 5 p.

1979a. Notes on a more generalized yield-per-recruit analysis for crustaceans using size-specific inputs. Fish. Mar. Serv. MS Rep. 1525: 40 p.

1979b. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the Southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 204–216.

CAMPBELL, A. 1983. Growth of tagged American lobsters, *Homarus americanus*, in the Bay of Fundy. Can. J. Fish. Aquat. Sci. 40: 1667–1675.

CAMPBELL, A., AND R. K. MOHN. 1983. Definition of American lobster stocks for the Canadian Maritimes by analysis of fishery-landing trends. Trans. Am. Fish. Soc. 112: 744–759.

CAMPBELL, A., AND D. G. ROBINSON. 1983. Reproductive potential of three American lobster (*Homarus americanus*) stocks in the Canadian Maritimes. Can. J. Fish. Aquat. Sci. 40: 1958–1967.

CAMPBELL, A., AND A. B. STASKO. 1985. Movements of tagged American lobsters, *Homarus americanus*, off Southwestern Nova Scotia. Can. J. Fish. Aquat. Sci. 42: 229–238.

CHITTLEBOROUGH, R. G. 1979. Natural regulation of the population of *Panulirus longipes cygnus* George and responses to fishing pressure. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 217–221.

CHITTLEBOROUGH, R. G., AND B. J. PHILLIPS. 1979. Recruitment to the catchable stock of the western rock lobster (*Panulirus longipes cygnus*) George. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 139–142.

CONAN, G. Y. 1975. A growth model of *Nephrops norvegicus* from Biscay Bay in function of periodicity of moult. Int. Cons. Explor. Mer C.M. 1975/K:10: 21 p.

CONAN, G. Y., AND K. R. GUNDERSEN. 1979. Growth curve of tagged lobsters (*Homarus gammarus*) in Norwegian waters as inferred from the relative increase in size at moulting and frequency of moult. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 155–166.

COOPER, R. A., AND J. R. UZMANN. 1971. Migrations and growth of deep-sea lobsters, *Homarus americanus*. Science (Wash., DC) 171: 288–290.

1977. Ecology of juvenile and adult clawed lobsters, and *Nephrops norvegicus*, p. 187–208. *In* B. F. Phillips and J. S. Cobb [ed.] Workshop on lobster and rock lobster ecology and physiology, Perth, Western Australia, 26 January – 1 February 1977. Circular No. 7, CSIRO, Division of Fisheries and Oceanography. 300 p.

CSIRKE, J., AND J. F. CADDY. 1983. Production modelling using mortality estimates. Can. J. Fish. Aquat. Sci. Vol. 40: 43–51.

CUSHING, D. H. 1975. The natural mortality of the plaice. J. Cons. Int. Explor. Mer 36(2): 150–157.

DOW, R. L. 1977. Relationship of sea surface temperature to American and European lobster landings. J. Cons. Int. Explor. Mer 37(2): 186–191.

ENNIS, G. P. 1978. Growth curves for Newfoundland lobsters from data on moult increment and proportion moulting. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 79/79: 11 p.

FAO/UNDP. 1983. Report of the Workshop on assessment of the shrimp stocks of the west coast of the Gulf between Iran and the Arabian Peninsula, Kuwait, 17–22 October 1981.

FLOWERS, J. M., AND S. B. SAILA. 1972. An analysis of temperature effects on the inshore lobster fishery. J. Fish. Res. Board Can. 29: 1221–1225.

FOGARTY, M. J., AND S. A. MURAWSKI. 1984. An evaluation of two delayed-recruitment models for crustacean fisheries. Int. Cons. Explor. Mer C.M. 1984/K:23: 17 p. (Mimeo.)

GARCIA, S. 1983. The stock–recruitment relationship in shrimps: reality or artifacts and misinterpretations? Oceanogr. Trop. 18(1): 25–48.

1985. Reproduction, stock assessment models, and population parameters in exploited shrimp populations. Paper presented to the 2nd Australian Prawn Seminar, Kooralbynn, Queensland, 22–26 October 1984.

GARCIA, S. M., AND L. LE RESTE. 1981. Life cycles, dynamics, exploitation and management of coastal penaeid shrimp stocks. FAO Fish. Tech. Pap. 203: 215 p.

HANCOCK, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P-V. Reun. Cons. Int. Explor. Mer 164: 113–131.

HANCOCK, D. H., AND E. EDWARDS. 1967. Estimation of annual growth in the edible crab (*Cancer pagurus* L.). J. Cons. 31: 246–264.

HARRIS, J. G. K. 1975. The effect of density-dependent mortality on the shape of the stock and recruitment curve. J. Cons. Int. Explor. Mer 36(2): 144–149.

HERRNKIND, W. F. 1977. Movement patterns in Palinurid lobsters, p. 209–244. *In* B. F. Phillips and J. S. Cobb [ed.] Workshop on lobster and rock lobster ecology and physiology, Perth, Western Australia, 26 January – 1 February 1977. Circular No. 7, CSIROP, Division of Fisheries and Oceanography. 300 p.

HIATT, R. W. 1948. The biology of the lined shore crab, *Pachygrapsus crassipes*. Randall. Pac. Sci. 2: 135–213.

HILBORN, R. 1979. Comparison of fisheries control systems that utilize catch and effort data. J. Fish. Res. Board Can. 36: 1477–1489.

INCZE, L. S., M. K. MCDOWELL, AND R. S. OTTO. 1986. Recruitment variability of juvenile red king crab, *Paralithodes camtschatica*, in the southeastern Bering Sea, p. 370–378. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

JONES, R. 1984. Assessing the effects of changes in exploitation pattern using length composition data (with notes on VPA and cohort analysis). FAO Fish. Tech. Pap. 256: 118 p.

KERR, S. R., AND R. A. RYDER. 1977. Niche theory and percid community structure. J. Fish. Res. Board Can. 34: 1952–1958.

KURATA, H. 1956. Increase in size at moulting in crustacea. Bull. Hokkaido Reg. Fish. Res. Lab. 18-22: 1956–1960.

LAVETT-SMITH, C. 1975. Analysis of a coral reef community: size and relative abundance. Hydro-lab. J. 3: 31–38.

LILLY, G. R. 1984. Predation by Atlantic cod on shrimp and crabs off northeastern Newfoundland in autumn of 1977–82. Int. Cons. Explor. Mer C.M. 1984/G:53: 25 p.

MANDELBROT, B. 1977. Fractals: form, chance, and dimension. Freeman Publications, San Francisco, CA.

MARCHESSAULT, G. D., S. B. SAILA, AND W. J. PALMA. 1976. Delayed recruitment models and their application to the American lobster (*Homarus americanus*) fishery. J. Fish. Res. Board Can. 33: 1779–1787.

MARK, D. M. 1984. Fractal dimension of a coral reef at ecological scales: a discussion. Mar. Ecol. Prog. Ser. 14: 293–294.

MAUCHLINE, J. 1976. The Hiatt growth diagram for custacea. Mar. Biol. 35: 79–84.

1977. Growth of shrimps, crabs and lobsters — an assessment. J. Cons. 37: 162–169.

MCLEESE, D., AND D. G. WILDER. 1958. The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. J. Fish. Res. Board Can. 15: 1345–1354.

METHOT, R. D. JR., AND L. W. BOTSFORD. 1982. Estimated preseason abundance in the Californian Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 39: 1077–1983.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL. 1982 Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia. Fish. Bull. 80: 475–486.

MORSE, D. R., J. H. LAWSON, M. M. DODSON, AND M. H. WILLIAMSON. 1985. Fractal dimension of vegetation and the distribution of arthropod body lengths. Nature (Lond.) 314: 731–733.

NEAL, R. A. 1975. The Gulf of Mexico research and fishery on penaeid prawns, p. 1–8. *In* P. C. Young [ed.] First Australian National Prawn Seminar, Maroochydore, Queensland, 22–27 November 1973, Canberra. Australian Government Publishing Service, Canberra.

OLINICK, M. 1978. An introduction to mathematical models in the social and life sciences. Addison-Wesley Publishing Company, Inc., Reading, MA. 466 p.

PALOHEIMO, J. E. 1963. Estimation of catchabilities and population sizes of lobsters. J. Fish. Res. Board Can. 20: 59–88.

PANAYOTOU, T. 1982. Management concepts for small-scale fisheries: economic and social aspects. FAO Fish. Tech. Pap. 228: FIPP/T228 (En). 53 p.

PAULY, D. 1980. A method to estimate the stock–recruitment relationship of shrimps. Trans. Am. Fish. Soc. 111: 13–20.

1984. Some simple methods for the assessment of tropical fish stocks. FAO Fish. Tech. Pap. 234: 52 p.

PHILLIPS, B. F., G. R. MORGAN, AND C. M. AUSTIN.1980. Synopsis of biological data on the western rock lobster, *Panulirus cygnus* George, 1962. FAO Fish. Synop. No. 128, Doc. FIR/S128: 64 p.

PRICE, A. R. G. 1982. Distribution of penaeid shrimp larvae along the Arabian Gulf coast of Saudi Arabia. J. Nat. Hist. 16: 745–757.

PRINGLE, J. D., G. J. SHARP, AND J. F. CADDY. 1982. Interactions in kelp bed ecosystems in the Northwest Atlantic: a review of a workshop. Can. Spec.

Publ. Fish. Aquat. Sci. 59: 108–113.
RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.
1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191: 382 p.
SASTRY, A. N., AND L. ZEITLIN-HALE. 1977. Survival of communally-reared larval and juvenile lobsters, *Homarus americanus*. Mar. Biol. 39: 297–303.
SCARRATT, D. J. 1973. Abundance, survival, and vertical and diurnal distribution of lobster larvae in Northumberland Strait, 1962–63, and their relationships with commercial stocks. J. Fish. Res. Board Can. 30: 1819–1924.
SHEPHERD, J. G. 1982. A versatile new stock–recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. Int. Explor. Mer 40(1): 67–75.
STAPLES, D. J., W. DALL, AND D. J. VANCE. 1981. Catch prediction of the banana prawn *Penaeus merguiensis* in the southeastern Gulf of Carpentaria. Paper presented at the Workshop on the Scientific Basis for the Management of Penaeid Shrimp, Key West, Florida, 18–24 November 1981.
SUTCLIFFE, W. H. JR. 1973. Correlations between seasonal river discharge and local landings of American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 30: 856–859.
URSIN, E. 1982. Stability and variability in the marine ecosystem. Dana 2: 51–67.
WALTERS, C. J., AND D. LUDWIG. 1981. Effects of measurement errors on the assessment of stock–recruitment relationships. Can. J. Fish. Aquat. Sci. 38: 704–710.

## Appendix: Fractals and Their Possible Relevance to Modelling Postrecruitment Processes for Crustacea

A fractal surface can be described as one which becomes disproportionately large as the unit of measurement is decreased. Most "rough" or dissected natural surfaces show this phenomenon to some degree, and Morse et al. (1985) suggested that such a fractal structure is ecologically important in that there is more useable space for smaller organisms occupying the surface than for larger ones, a conclusion of obvious relevance to recruitment studies. The relevant question in this latter context, however, is how competition or predation increases as an organism grows from settlement to maturity on such a surface. This is the question addressed in a preliminary way in this appendix.

Assuming the simplest case, that a postsettlement surface appoximates to a fractal, then from Morse et al. (1985) we should expect in examining a cross-section of the substrate that whatever the magnification it is viewed at, "whether the line represented a 1 m or 100 km stretch, the appearance would be the same" (Mark 1984). Recognizing, as did Bradbury et al. (1984) that for some biological systems (e.g. coral reefs), it is precisely departures from this axiom at different scales that may be of major biological importance, it is nonetheless interesting to pursue a development assuming first that settlement surfaces approximate to a fractal and write after Morse et al. (1985)

$$\text{(A.1)}\quad \text{Log } N(L) = D \log(1/L) + \log k$$

where $N(L)$ is the number of squares of dimension $L$ that the tracing of an outline of the cross-section of a surface enters, given size of grid units $L$, $k$ a constant, as is $D$, the fractal dimension (see Morse for illustration).

For coral reefs, Bradbury et al. (1984) found values for $D$ over scales of 10–1000 cm ranging from 1.05 to 1.15, surprisingly low compared with terrestrial vegetation, where although not over a comparable scale, Morse et al. (1985) found values of $D$ over a range of 1–100 mm of 1.28–1.79. Evidently, for higher values of $D$, the available surface drops off more rapidly with dimension (and hence size and age of organism); this has obvious implications for mortality processes.

The above description from Mark (1984) implies that for a surface approximating to a fractal, at any magnification there should be the same number of crevices or "physical niches" present per unit linear measurement of a series of cross-sections irrespective of the unit measure being used to "step off" the length of the cross-sectional outline. The direct measurement of the actual value(s) of $D$ may in practise be difficult, but Morse et al. (1985), in discussing terrestrial vegetation, suggested that looking at the actual size spectrum of (in this case) interstitial organisms may, from the log–log plot of numbers against size, give some indication of the value(s) of $D$ that apply for a given size interval.

It is then postulated that the number of crevices $C(L)$ suitable for occupation by an individual of size $L$ (e.g. Fig. 5) in a given cross-section of the settlement surface is given by

$$\text{(A.2)}\quad \log C(L) = D \log (1/L) + \log k'$$

where $k'$ is a constant.

The interesting question is, then, what is the rate of decline in number of crevices with size and age for an organism that (for the sake of convenience) has a growth rate defined by the von Bertalanffy growth equation, and where growth rate is not influenced by the availability or otherwise of suitable substrate (niches); assuming again in the simplest case, that crevice dwelling is an obligate condition? Thus, if all available crevices of dimension $L$ are filled with individual organisms of the same linear dimensions, we can redefine $N(L)$ as the number of individuals of size $L$ occupying crevices of the same general dimension, in the confidence that as they increase in size, the numbers of appropriate sized niches will be always less than the potential number of occupants (the "musical chairs" analogy). Since it is reasonable to assume under niche-limited conditions that a larger animal that can fit in a given niche will supplant a smaller one, the possibility that small animals could fill vacant larger niches is not addressed in this preliminary treatment. Equation A.2 can then be rewritten for size $L$ as

$$N(L_1) = k'/L^D.$$

For all crevices of dimension $L$ to be identified by parallel transects across the occupied surface, these transacts would have to be spaced $L$ units apart, i.e. for a flat (rectangular) surface with straight line width $k''$, the number of parallel transects is given by $k''/L$.

Hence, the number of crevices (and number of organisms $N(L)$ of dimension L) on this surface is given by

$$N(L) = (k'/L^D)\,(k''/L) = k'''/L^{D+1}$$

where $k''' = k'k''$, i.e.

$$\text{(A.3)}\quad N(L_1) = k'''/L_1^{D+1}.$$

But for a prerecruit lobster, for example, only exposed to natural deaths if displaced from a crevice.

$$N(L_2) = N(L_1) \exp - M_L \cdot \Delta t$$

and

$$\text{(A.4)}\quad M_L \cdot \Delta t = \log_e (N(L_1)/N(L_2))$$

where $\Delta t$ is the time taken to grow from size $L_1$ to $L_2$. Substituting for $N(L_n)$ (Equation A.3 into Equation A.4) gives

$$M_L \cdot \Delta t = \log_e (L_2^{D+1} L_1^{D+1})$$

and since the von Bertalanffy equation gives on transformation $\Delta t = (1/K) \log_e((L_\infty - L_1)/L_\infty - L_2))$ ($K$ and $L_\infty$ being the von Bertalanffy growth coefficient and maximum size, respectively),

$$M_L = \frac{K \cdot \log_e (L_2^{D+1}/L_1^{D+1})}{\log_e (L_\infty - L_1)/(L_\infty - L_2))}.$$

# Effects of Environmental Forcing on Age-Structured Populations: Northern California Dungeness Crab (*Cancer magister*) as an Example

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Evaluation of potential environmental effects on recruitment requires knowing how environmental forcing can affect recruitment and subsequent catch, and how these effects depend on life history. General relationships between a time series of an environmental forcing variable, the resulting time series of recruitment, and the subsequent time series of catch or abundance are described here for a fishery in which environmental forcing affects density-dependent recruitment and the population is fished at a constant rate. For a stable population with overcompensatory, density-dependent recruitment, the recruitment time series will resemble the environmental time series except that frequencies near $1/(2 \times$ mean age in the population) will be emphasized. The amount of selective emphasis will depend on the degree of overcompensation, harvest rate, and width of the cohort size distribution (in a size-selective fishery). For a population harvested at constant rate, the catch time series will resemble the recruitment time series except that lower frequencies will be emphasized. The degree of selective emphasis will depend on harvest rate and width of the cohort size distribution. Application of these results to Dungeness crab (*Cancer magister*) research has allowed analysis of combined effects of density dependence and environmental forcing. They show (1) that criteria formerly used to evaluate density-dependent recruitment mechanisms were too strict, (2) that female harvest could reduce harvest variability due to environmental forcing, and (3) how a nonlinear influence of spring wind stress in combination with density-dependent recruitment could cause the observed catch record. Implications for other crustacean populations are discussed.

Pour évaluer les effets potentiels de l'environnement sur le recrutement, il est nécessaire de savoir comment les forces environnementales peuvent affecter le recrutement et les captures subséquentes, et dans quelle mesure ces effets dépendent du cycle biologique. Nous décrivons ici les relations générales entre une série chronologique portant sur une variable environnementale, la série chronologique du recrutement qui en résulte et la série chronologique subséquente portant sur les captures ou l'abondance, pour une pêche dans laquelle les forces environnementales affectent le recrutement dépendant de la densité et dans laquelle la population est exploitée à un rythme constant. Pour une population stable présentant un recrutement de surcompensation dépendant de la densité, la série chronologique du recrutement ressemblera à celle de la variable environnementale, mais les fréquences proches de $1/(2 \times$ âge moyen de la population) seront accentuées. L'importance de l'accentuation sélective dépendra du degré de surcompensation, du taux de prélèvement et de la largeur de la distribution par taille des cohortes (dans une pêche à sélection par la taille). Dans une population exploitée à rythme constant, la série chronologique des captures ressemblera à celle du recrutement, mais les fréquences les plus basses seront accentuées. Le degré d'accentuation sélective dépendra du taux de capture et de la largeur de la distribution par taille des cohortes. L'application de ces résultats à la recherche sur le crabe dormeur (*Cancer magister*) a permis d'analyser les effets combinés de la dépendance à l'égard de la densité et des forces environnementales. Ces études montrent : 1) que les critères utilisés jusque-là pour évaluer les mécanismes de recrutement dépendant de la densité étaient trop stricts, 2) que le prélèvement des femelles pourrait réduire la variabilité des captures due aux forces environnementales, et 3) que l'influence non linéaire de la tension du vent au printemps, combinée au recrutement dépendant de la densité, pourrait expliquer la structure des captures observée. Nous examinons les incidences de cette analyse sur d'autres populations de crustacés.

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Factors that govern recruitment to populations are a major concern in fisheries research because cohort strength is believed to be determined at young ages. This belief is generally supported by the existence of a "critical phase" for fish larvae (Hjort 1914) and by the fact that larvae of fish and crustaceans are relatively immotile and subject to the vagaries of fluctuating physical conditions and possible transport over long distances. Because of the importance of recruitment, considerable effort is spent determining the factors responsible for fluctuations in recruitment. Determination of these factors is particularly difficult because, in addition to possible density-dependent factors, physical environmental variables may also have a substantial effect on recruitment. The latter phenomenon is referred to here as environmental forcing.

One approach to describing recruitment is to use population data such as estimates of recruitment and abundance to empir-

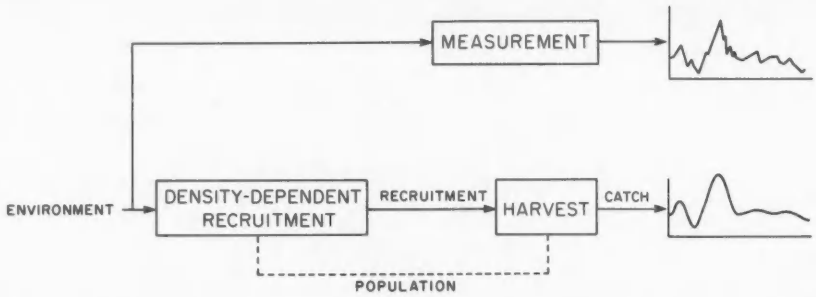


FIG. 1. Schematic view of the problem of determining whether an environmental variable has an effect on an observed catch record.

ically describe the way in which recruitment varies with stock, and to treat environmentally induced fluctuations as random noise of unknown origin. The dependence of recruitment on adult stock usually is described by a relationship of either the Ricker (1954) or the Beverton and Holt (1957) type. There are also general stock–recruitment models that include these two types (e.g. Shepherd 1982; Schnute 1985) as well as formal harvest strategies for adaptively determining the shape of the curve (Walters 1981). The behavior of the deterministic models is reasonably well understood for both semelparous species (Ricker 1954) and iteroparous species for which age structure is important (Ricker 1954; Allen and Basasibwaki 1974; Botsford and Wickham 1978; and others). The effect of noise on stock–recruitment models often is ignored, but also has been analyzed by adding white noise (i.e. noise having no intraseries correlation) to simple stock–recruitment models (e.g. May et al. 1978) and to those with age structure (Horwood and Shepherd 1981; Horwood 1983, 1984; Reed 1983).

Another approach to this problem is to attempt to identify the environmental variable actually responsible for the random variability in recruitment and then to describe the actual physical and biological mechanisms of recruitment. This approach usually involves statistical analysis of the relationship between time series of environmental data and an estimate of recruitment, catch, or abundance. This analysis can be carried out in several ways. One way is to compute time-lagged correlations between population data (recruitment if possible) and potential environmental factors to determine which environmental factors are similar enough to population fluctuations to be considered further (e.g. Botsford and Wickham 1975; Mathews and Olson 1980; Scarnecchia 1981, 1984). Another way is to fit a model to population and environmental data and retain those environmental variables that contribute significantly to the fit. This may be a linear regression of either recruitment, recruitment per spawner, or expected recruitment (on the basis of a stock–recruitment curve) on potential environmental variables, or it may be a general nonlinear estimate of population parameters (e.g. Nelson et al. 1977; Parrish and MacCall 1978; Bakun and Parrish 1983; Reish et al. 1985; Anthony and Fogarty 1985; Stocker et al. 1985).

Correct performance of these computations and valid interpretation of the results require knowledge of the general relationship between environmental variables and recruitment, catch, or abundance. Since the environment affects recruitment, which is also possibly influenced by density-dependent mechanisms, and catch and abundance include several cohorts (i.e. the combined effect of recruitment in several years), population variables cannot be expected to vary in exactly the same way that the environmental forcing variable does. As a result, the correlation between an environmental variable and a population variable would not be expected to be 1.0, even if an accurately measured environmental variable were completely responsible for accurately measured abundance. Clearly, the nature of such a relationship depends on the processes that take place between the point in the life history at which the environment affects recruitment to the population and the point at which that effect influences catch or abundance. This relationship is the subject investigated here.

The situation faced when attempting to determine the influence of the environment on recruitment is depicted in Fig. 1. We observe a time series of a measurement of an environmental variable and an estimate of a population variable (usually catch or recruitment). Determination of whether fluctuations in the former are the cause of fluctuations in the latter (i.e. environmental forcing) requires understanding the processes that may occur between them. We examine here the way in which differences in life history, form of the density-dependent recruitment relationship, and harvest rate affect the way in which recruitment, catch, and abundance are influenced by environmental forcing variables.

The work described here arose from research to determine the cause of cyclic fluctuations in catches of Dungeness crab (*Cancer magister*) on the west coast of the United States (Botsford 1986). Briefly, several density-dependent recruitment mechanisms (e.g. cannibalism, predation by an egg-predator worm, density-dependent fecundity or larval survival) have been investigated and some of them remain as possible causes. Statistical analyses of similarities between the catch record and several environmental variables (e.g. upwelling, temperature, number of sun spots, and wind stress) have led to proposals that they cause the cycles.

## Models

Determination of a general mathematical description of the interaction of recruitment (to the population) and the environment is inherently difficult because of the wide variety of species and actual mechanisms. Density dependence may occur as early as in female fecundity or as late as during the first several months of the postlarval phase (e.g. cannibalism), and the environment may affect this process at any point in between. The first critical issue is separation of the effects of egg production from density dependence. Most stock–recruitment models incur a lack of realism by forcing egg production and

density dependence to depend on the same function of the adult stock (usually biomass or total fecundity). Since the way in which juveniles and adults affect egg production is not generally the same as the way in which they affect density-dependent recruitment, separate age-weighting functions are used here for each. A second critical issue is whether total annual egg production always will be above a limited carrying capacity of the larval environment, so that, for all practical purposes, the number of surviving eggs each year will appear not to depend on adult stock. This aspect is optional in the model used here:

$$(1) \quad R_{t+1} = B_t f_D[C_t] f_N[N_t]$$

in which $R_{t+1}$ = recruitment rate, $B_t$ = total egg production rate, $f_D[\cdot]$ = a density-dependent survival function, $f_N[\cdot]$ = an environment-dependent survival function. $C_t$ = the effective population size as it affects density-dependent recruitment in year $t$, and $N_t$ = an environmental forcing variable in year $t$. In this model, both $B_t$ and $C_t$ are weighted sums over adult stock:

$$(2a) \quad B_t = \sum_{a=1}^{T} n_{a,t} b_a$$

$$(2b) \quad C_t = \sum_{a=1}^{T} n_{a,t}\, c_a$$

where $b_a$ = fecundity at age $a$, $c_a$ = the effect of an individual at age $a$ on density-dependent recruitment, $n_{a,t}$ = the number of individuals between age $a$ and $a + da$ at time $t$, and $T$ = maximum age in the population. An alternate form of this model is to consider $B_t$ to be a constant, $B_c$, assuming that total annual egg production is higher than the larval carrying capacity.

The relationship between recruitment and catch or adult abundance must also be modeled. If one can assume that post-recruitment mortality is non-time-varying, then both catch and abundance are weighted sums of past values of recruitment:

$$(3a) \quad \mathrm{Ca}_t = H \sum_{i=a_c}^{T} \sigma_i R_{t-i}$$

$$(3b) \quad A_t = \mathrm{C}_t / H$$

where $\mathrm{Ca}_t$ = catch at time $t$, $A_t$ = harvestable abundance at time $t$, $\sigma_i$ = survival to age $i$ (including fishing mortality), $H$ = harvest rate, and $a_c$ = age of first capture. This expression becomes more complicated for the case in which only individuals greater than a certain size are harvested and there is a distribution of sizes at each age. In this case, a cohort enters the fishery over several years, rather than in one year. The expression for catch is

$$(4) \quad \mathrm{Ca}_t = H \sum_{i=1}^{T} a_i\, \sigma_i\, \mathrm{R}_{t-i}$$

where

$$a_i = \sum_{j=1}^{T} p_j\, h_{i-j}$$

where $p_j$ = the fraction of a cohort that reaches legal size at age $j$ and

$$h_i = (1 - H)^i \qquad i > 0$$
$$= 0 \qquad i < 0$$

and $\sigma_i$ does not include fishing mortality. See Botsford (1984) for the rationale behind this expression.

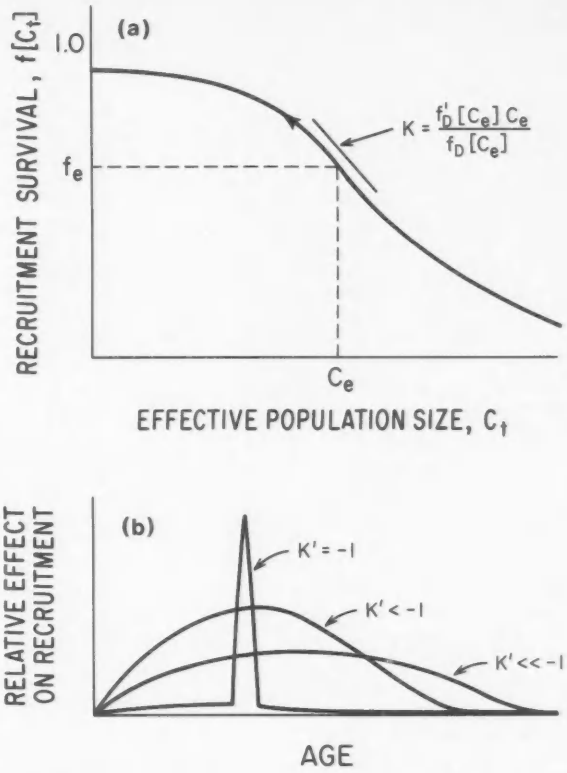


FIG. 2 (a) Dependence of survival to recruitment on adult population size ($f_D[\cdot]$), and the definition of $K$, the normalized slope of this function at equilibrium ($C_e$, $f_e$). Arrowhead indicates direction in which equilibrium moves with increasing female harvest. (b) Effect of age structure on $K'$, the stability limit of $K$.

## Effects of Density-Dependent Recruitment and Harvest

These models can be used to describe, in a general way, how a random environmental variable that affects recruitment will influence the resulting recruitment, catch, and abundance time series. This problem will be discussed in two steps: we first consider the effect of the environment on recruitment and then the effect of recruitment on catch or abundance (cf. Fig. 1).

### Stability

For the description of the effect of environment on recruitment we use a similar mathematical approach to that taken earlier to the analysis of stability of age-structured models with density-dependent recruitment (Botsford and Wickham 1978). Because results described here regarding the influence of environment on these models are closely related to earlier stability results, a brief review is worthwhile. Botsford and Wickham (1978) linearized a deterministic version of equation (1) about its equilibrium value to determine the population characteristics that would cause cycles in recruitment. They found that whether recruitment was cyclic depended on two parameters: (1) the normalized slope ($K$) of the recruitment survival function ($f_p[\cdot]$) and (2) a parameter ($K'$) that depends on the age structure of the population as it affects density-dependent re-

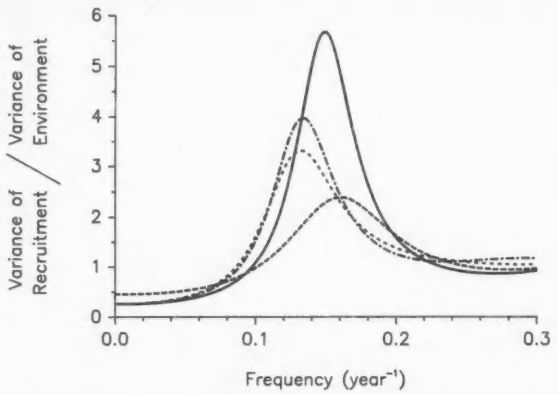


FIG. 3. Ratio of variance in recruitment to variance in incremental environmental noise at each frequency for the baseline case (harvest rate $H = 0.8$, normalized slope of the recruitment survival function $K = -2.0$, and cohorts completely enter the fishery in 1 yr (—), cohorts enter the fishery over several years (-·-), $H = 0.5$ (---), and $K = -1.5$ (– – –).

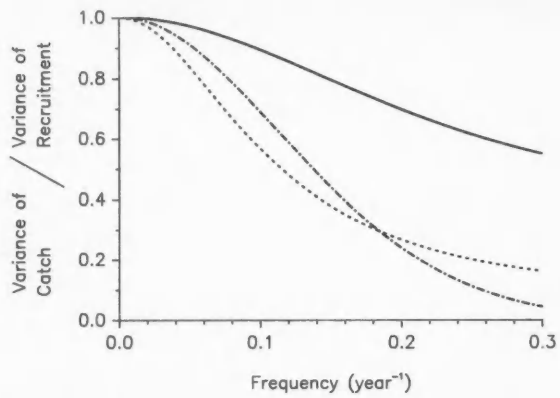


FIG. 4. Ratio of variance in catch to variance in recruitment at each frequency for the baseline case (harvest rate $H = 0.8$ and cohorts completely enter the fishery in 1 yr) (—), $H = 0.5$ (---), and cohorts enter the fishery over several years (-·-).

cruitment (Fig. 2). A steep slope of the recruitment survival function (i.e. a more negative value of $K$) and a narrow age structure (i.e. a more positive value of $K'$) both lead to a less stable population (i.e. one that is more likely to produce cycles). A population actually becomes unstable (i.e. produces cycles) when the value of $K$ is less than $K'$. The period of the cycles is approximately twice the mean age of the population.

The effect of life history parameters on whether a population will cycle in the absence of environmental forcing can be inferred from these results. Because size-selective harvest will remove older age classes, thereby narrowing the age distribution and lowering the mean age, it will tend to make the population less stable and will lower the period of cycles, if any are produced. Because a wider cohort size distribution in a size-selective fishery will broaden the age structure, it will lead to a more stable population, and will change the period of potential cycles, if it leads to a different mean age (Botsford 1984).

Stability conditions are similar for the model with assumed constant egg production ($B_t = B_c$) except that values of $K'$ are more positive by approximately 1.0 (Botsford and Wickham 1978).

## Environmental Forcing

The way in which an environmental variable affects recruitment is related to these deterministic stability results, and hence can also be related to life history characteristics. The description of the effect of a random environment on recruitment is based on the fact that random time series can be described in terms of their variance at each frequency (i.e. their spectrum). This description is based on results of an analysis of a linearized version of the recruitment model in equation (1) (L. W. Botsford and J. Brittnacher, in prep.). A useful characteristic of linear systems is that variance at any frequency in the input (here the environmental variable) will cause variability only at that frequency in the output (here the recruitment). Using this, a general way of describing how an environmental variable influences recruitment in a stable population (i.e. one that would not be cycling according to the above deterministic stability analysis) is to express the ratio of the variance at each frequency in the recruitment time series to the variance at each frequency in the time series of the environmental variable.

An example for parameter values that correspond roughly to Dungeness crab is shown in Fig. 3. For the baseline case shown in Fig. 3, the recruitment system is more sensitive to variance at certain frequencies. Specifically, it is most sensitive to frequencies near the frequency at which the population would cycle in the absence of environmental forcing if it were unstable (i.e. $1/(2 \times$ mean age)). This means that if a stable population is influenced by an environmental variable, variance in the time series of the environmental variable at frequencies near $1/(2 \times$ mean age) will induce a larger variance in the recruitment time series (at the same frequency) than will variance at other frequencies in the environmental series. For example, if the spectrum of the environmental variable were flat (i.e. equal variance at all frequencies), the spectrum of the recruitment function would be that shown in Fig. 3.

Changes in the "frequency response" of the recruitment system with changes in life history parameters are similar to those expected on the basis of stability results. As the normalized slope ($K$) of the recruitment survival function becomes shallower (which would lead to a more stable population), the response is less peaked. As size-selective harvest decreases from $H = 0.8$ to $H = 0.5$) (which would lead to a more stable population and higher period), the response is less peaked and the peak frequency decreases. As the width of the size distribution increases so that instead of all becoming harvestable at age 4, individuals enter the harvestable size range at ages 3, 4, 5, and 6 (10, 40, 40, and 10%, respectively) (which would lead to a more stable population and longer period), the response becomes less peaked and the peak moves to a lower frequency.

A similar analysis of the effect of environment on recruitment for the model with total egg production assumed constant (i.e. $B_t = B_c$) is similar except that the values of $K$ leading to equivalent behavior are more positive by 1.0.

The next step, the relationship between recruitment and catch or abundance, can be described in a similar way. For constant harvest rate, catch and abundance differ only by the factor $H$; hence, only catch is discussed here. A plot of the ratio of variance at each frequency in the recruitment time series to the variance at each frequency in the catch time series is shown

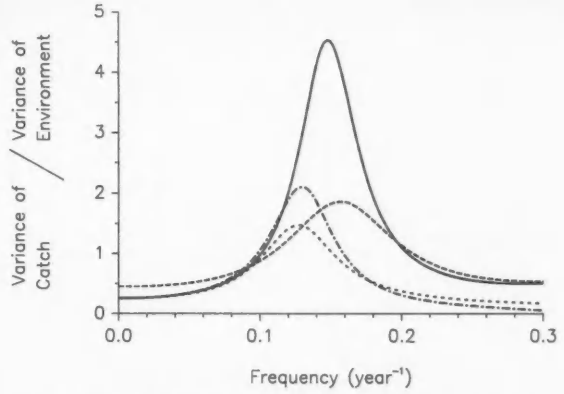


FIG. 5. Ratio of variance in catch to variance in incremental environment at each frequency for the baseline case (harvest rate $H = 0.8$, normalized slope of the recruitment survival function $K = -2.0$, and cohorts completely enter the fishery in 1 yr) (—), cohorts enter the fishery over several years (-·-), $H = 0.5$ (---), and $K = -1.5$ (— — —).

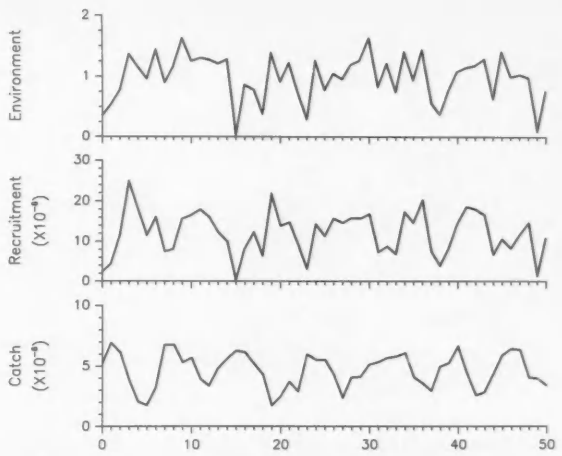


FIG. 6. Simulation of the model used to generate Fig. 3, 4, and 5 for $K = -2.5$ and $H = 0.5$ and all males are legal size at 4 yr.

in Fig. 4. As seen in the figure, the time series of catch will differ from the time series of recruitment in that variance at higher frequencies in the recruitment series will not show up in the catch series. This effect is more pronounced at low harvest rates. The effects of this relationship are known to many fishery managers. At low harvest rates, fishing involves catching the sum of several age classes; hence, the catch time series does not resemble recruitment, but rather is smoother. At higher harvest rates, catch is primarily from a single age class, and hence resembles recruitment several years earlier. An example would be the intensely exploited fisheries for the American lobster (*Homarus americanus*) in New England. Note that Fig. 4 indicates that high frequencies are suppressed at harvest rates of $H = 0.5$ (resulting in smoothing) and that all frequencies are affected approximately equally (resulting in recruitment closely resembling catch) at a high harvest rate of $H = 0.8$. As the width of the cohort size distribution changes, cohorts enter the fishery gradually, and again, variance at higher frequencies in recruitment does not appear in catch.

To describe the relationship between an environmental variable and catch, one would combine the effect of density-dependent recruitment (Fig. 3) with the effect of harvest (Fig. 4). The frequency-dependent sensitivity of catch to an environmental variable is the product at each frequency of the curves in Fig. 3 and 4 (Fig. 5).

A simulation with $K = -2.5$ and $H = 0.5$ and all individuals becoming harvestable at age 4 (Fig. 6) illustrates the effects described by Fig. 3, 4, and 5. The environmental forcing function is an uncorrelated (white) random series. Note that where fluctuations near 6 or 7 yr in period randomly occur in the time series of the environmental forcing variable, they are emphasized in the recruitment time series. Note also that catch lags recruitment by 4 yr and is slightly smoother.

## Implications for Dungeness Crab

These results provide analytical means of extending evaluation of the causes of cycles in Dungeness crab catch to combinations of density-dependent and environmental forcing mechanisms. In work thus far, hypothetical density-dependent mechanisms have been evaluated using results of stability analysis. Field data on life history characteristics relevant to each proposed causal mechanism have been used to determine essentially (1) whether $K$ is less than $K'$ and (2) whether the period of cycles that would be produced match those observed in the catch record (Botsford 1986). Environmental mechanisms have been evaluated by computing cross correlations between potential environmental forcing variables and catch, and by computing autocorrelations of environmental forcing variables to determine whether they are as cyclic as the catch record (e.g. Botsford and Wickham 1975; Johnson et al. 1986). Considering these two classes of mechanisms to be acting in concert rather than separately has led to several new insights that allow more realistic evaluation of the various hypotheses.

One point suggested by the environmental forcing analysis is that because stable populations can exhibit behavior that is dominated by a single frequency even without a cyclic forcing variable (e.g. from the peaked response in Fig. 3), the requirement that proposed density-dependent mechanisms must be able to produce instability (i.e. $K$ must be less than $K'$) is perhaps too demanding. To test this, stable populations with various values of $K$ and with recruitment influenced by an environmental forcing variable with a flat spectrum (i.e. white noise) were simulated. Autocorrelations of the output were computed to compare them with the autocorrelation of the observed catch record (Fig. 7). Since a value of $K$ of approximately $-2.5$ produces an autocorrelation that is as cyclic as that of the observed catch record (for which the autocorrelation declines to $-0.566$ then increases to $+0.539$; Johnson et al. 1986), the requirement that $K = -3.5$ (the value that would be necessary for unstable cycles) for a mechanism to be causing the observed cycles is not realistic.

A second inference from the environmental forcing analysis is a rough idea of how closely one should expect an environmental forcing variable to resemble the catch record. Botsford (1986) noted that although the time series of spring wind stress was significantly correlated with catch and was itself cyclic (Johnson et al. 1986), it did not closely resemble the catch record. To test whether it could indeed be causing the cycles, he simulated several configurations of the population (with and

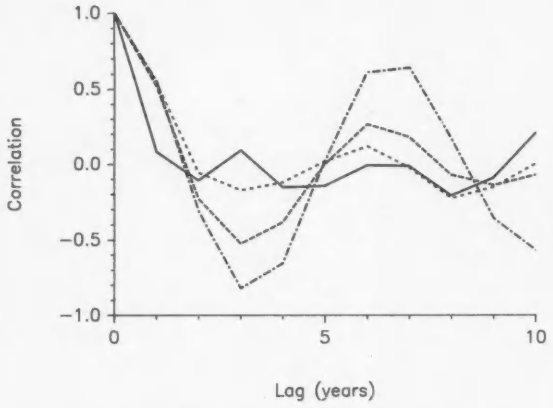


FIG. 7. Changes in autocorrelation of catch in a population model with density-dependent recruitment influenced by an uncorrelated (white) environmental variable as the normalized slope of the recruitment survival function ($K$) is varied. Lines correspond to the environmental variable (—), catch with $K = -1.0$ (- - -), catch with $K = -2.0$ (— — —), and catch with $K = -3.0$ (-·-).

without density dependence) using spring wind stress as the environmental forcing variable. Since several combinations of a nonlinear effect of the wind stress and density dependence could produce a time series that approximated the observed catch record, the wind forcing hypothesis could not be rejected. As suggested by the analysis described here, even without density dependence, the effects of harvest "removed" the higher frequencies in the wind signal, and with density dependence, frequencies near the observed frequency were "selected for."

A third insight from the environmental forcing analysis regards the possible effect of single sex harvesting. When only males are harvested and their harvest does not affect the number of eggs produced by each female (i.e. $b_a$), equilibrium level of effective population size (i.e. $C_t$ in equation (2b)) will not change. However, when females are also harvested, equilibrium population size decreases (see arrowhead on Fig. 2a). Because $K$ is the normalized slope of the recruitment survival function at equilibrium, a decline in equilibrium population size causes $K$ to increase. From the environmental forcing analysis, an increase in $K$ reduces the sensitivity of recruitment to environmental forcing. Thus, female harvest reduces equilibrium population level and the influence of the environment on recruitment. This makes sense biologically. As the population level is reduced below carrying capacity, density-dependent effects are less likely to exacerbate environmental perturbations. The implication for Dungeness crab is that by having a harvest policy that does not control population level (i.e. a males-only harvest), we may be missing an opportunity to reduce the fluctations in recruitment and harvest caused by environmental forcing.

## Discussion

Under the assumptions made here, it appears that the nature of the recruitment survival function and other life history characteristics govern the way in which the random environment in the prerecruit stages ultimately affects recruitment. These results may be useful in general, both in research to determine the causes of fluctuations in crustacean recruitment and in projection of changes in harvest variability from proposed changes in harvest policy. The extent to which they prove useful depends on the prevalence of populations that fulfill the assumptions under which they were derived.

The "strength" of density-dependent recruitment survival (i.e. how negative $K$ is) is a major determinant of how environmental fluctuations will affect recruitment. The mildest form of density dependence, a stock–recruitment curve of the Beverton and Holt type (i.e. without a descending righthand limb), corresponds to a value of $K = -1.0$ for the model in equation (1). From Fig. 3, one would surmise that at $K = -1.0$ the frequency response would be flat, indicating that fluctuations in the environmental variable would appear in the recruitment time series. This is what one would expect a priori by considering the maximum recruitment level of a Beverton and Holt curve to be multiplied by a random environment. However, as the righthand limb of the recruitment curve declines, the recruitment time series does not closely resemble the time series of the environmental variable, but rather frequencies near $1/(2 \times$ mean age) are emphasized in the recruitment series. Thus, the results will be of most use in situations in which the stock–recruitment curve has a descending righthand limb. This is the case for at least two of the mechanisms proposed for Dungeness crab: cannibalism and predation by an egg-predator worm.

Both density-dependent recruitment and oceanographic conditions are thought to influence American lobster populations (Fogarty and Idoine 1986; Ennis 1983; Caddy 1979b). The relative constancy of landings (at least in some locations, e.g. the Gulf of Maine) and comparison of a set of data on fourth-stage larval abundance with later recruitment suggest that the stock–recruitment relationship is of the Beverton and Holt type (see Fogarty and Idoine 1986). If it actually is, fluctuations in an environmental variable that affects maximum recruitment will appear undistorted in the recruitment time series. Oceanographic conditions also appear to contribute to variability in postlarval settlement of the western rock lobster (*Panulirus cygnus*) (Phillips 1981) and there appears to be a stock–recruitment relationship with a descending limb at the puerulus stage (Morgan et al. 1982). Later stages may be of the Beverton and Holt type (see Ford et al. 1985) which could obscure or distort variability introduced in earlier stages.

A second determinant of how environmental variability will affect recruitment is the way in which the population is harvested. Size-selective harvesting makes the population more sensitive to environmental variability at specific frequencies if only males are harvested. However, if females are also harvested, in addition to effects on age structure that increase sensitivity, the equilibrium population level will also decline which reduces sensitivity of the population to environmental fluctuations. From this, one would expect that, all other things being equal, populations with density-dependent recruitment and environmental forcing in which both males and females are harvested would be less variable than similar populations in which only males are harvested.

In addition to its effect on the relationship between the environment and recruitment, harvest also affects the relationship between recruitment and catch. That the catch record will resemble the recruitment record only at high harvest rates is known to some fishery managers and scientists. The effect of nonzero width of the cohort size distribution in a size-selective

fishery becomes obvious when considering a highly exploited fishery such as that for American lobster in New England in which each cohort enters the fishery over several years. For crustacean fisheries, accurate description of this effect will require growth models that describe the effect of variability in the discrete growth process (i.e. molting) on the shape of the size distribution (see Shepherd et al. 1985; Botsford 1985).

Since the results regarding the relationship between the environment and recruitment were derived for a linearized model that was stable, they apply only to populations for which those assumptions are met. Whether linearization applies depends on the shape of the recruitment survival function and the amplitude of fluctuations under consideration. For relatively smooth recruitment survival functions and fluctuations with a coefficient of variation of up to 0.5, they will probably apply. Beyond that range, nonlinear effects introduce distortion not accounted for here. The range of values of $K$ for which the results apply strictly is from $-1.0$ to $K'$. When $K$ is less than $K'$, either limit cycles will occur (cf. Oster 1977; Gurney et al. 1980) or the system will be chaotic, and these results would not apply. As a population is harvested at higher rates, it may eventually move to a level that is essentially on the lefthand ascending limb of the stock–recruitment curve. This corresponds to a value of $K$ greater than $-1.0$ and results derived here would not apply. This appropriate model at that point would be a linear demographic model with random effects (e.g. see Cohen et al. 1983).

The relationship between recruitment and catch was based only on the assumption of constant harvest; hence, results can be expected to apply where that is approximately true.

The analysis described here is similar to earlier work by Horwood and Shepherd (1981), Horwood (1983, 1984), and Reed (1983) aimed at determination of the overall level of environmental noise on catch, except that they dealt only with uncorrelated (white) noise in recruitment. The level of variability due to uncorrelated noise would be proportional to the area under the curves in Fig. 5. Reed (1983) emphasized that harvest has two effects: (1) a dynamic effect on age structure (i.e. in Fig. 5) and (2) an effect on equilibrium. As noted here, the latter does not occur in a males-only harvest in which fecundity is not affected. Both of these increase variability in the harvest.

The applicability, usefulness, and refinement of the ideas developed here will depend on better understanding of actual crustacean recruitment systems. Environmental forcing through wind transport has been implicated in several: the blue crab (*Callinectes sapidus*) in Chesapeake Bay (Johnson 1982; Johnson et al. 1984) and penaeid shrimp in the Gulf of Carpentaria in Australia (Rothlisberg 1982). Wind has also been implicated through upwelling concomitant with reduced temperature in recruitment of pink shrimp (*Pandalus jordani*) (Rothlisberg and Miller 1983). Better understanding of recruitment may be accelerated by the study of small local populations for which detailed measurements can be made. An example of such a study is the work of Roughgarden et al. (1985) on a sessile crustacean, the barnacle *Balanus glandula*. They analyzed a model of recruitment to intertidal rocks, similar to the model given here, but with a constant supply of larvae (i.e. $B_t = B_c$) and a specific density-dependent recruitment mechanism, space-limited recruitment. Their analysis indicated that stability declined (i.e. $K$ became more negative) as the density of larvae available for settlement increased. This behavior was reflected in the actual populations. Through computation of autocorrelation of field samples of recruitment, they have found cyclic behavior on the seaward rocks (with higher larval densities) and no cycles on the inshore rocks (with lower densities).

Although Fig. 3–6 were generated from a model of the northern California Dungeness crab fishery and used to demonstrate general concepts as well as several changes in approach to analysis of that population, the model used does not completely reflect our current view of this population. Effort was assumed to be constant when it in fact varies in response to abundance (Botsford et al. 1983). Also, the weighting function for density-dependent recruitment ($c_a$ in equation (2b)) was assumed to be proportional to individual metabolic rate at age $a$. The true function will depend on the actual mechanism.

The current state of research on Dungeness crab population dynamics has some characteristics that may apply to other species (especially those in which cycles of unknown origin are present; cf. Caddy 1979a). There are currently several unrefuted density-dependent causal mechanisms and a cyclic environmental forcing mechanism, spring wind stress (Botsford 1986; Johnson et al. 1986). This lack of resolution is further complicated by the results obtained here which indicate that not only is each of these a possibility, but that a combination of varying levels of density-dependent and environmental forcing is also a possibility. From population level and environmental data it is difficult, if not impossible, to determine which combination is responsible for the cycles in catch. Further direct research on mechanisms, or adaptive management (i.e. attempting to hold density constant and observing the effect on variability), will be necessary to resolve this issue.

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## References

ALLEN, R. L., AND P. BASASIBWAKI. 1974. Properties of age structure models for fish populations. J. Fish. Res. Board Can. 31: 1119–1125.

ANTHONY, V. C., AND M. J. FOGARTY. 1985. Environmental effects on recruitment, growth, and vulnerability of Atlantic herring (*Clupea harengus harengus*) in the Gulf of Maine region. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 158–173.

BAKUN, A., AND R. H. PARRISH. 1983. Environmental inputs to fishery population models for eastern boundary current regions. *In* G. D. Sharp [ed.] Workshop on the effects of environmental variation on the survival of larval pelagic fishes. IOC Workshop Rep 28: 67–104.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. U.K. Minist. Agric. Fish. Fish. Invest. (Ser. 2) 19: 533 p.

BOTSFORD, L. W. 1984. Effect of individual growth rate on expected behavior of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 41: 99–107.

1985. Models of growth. *In* A. Wenner [ed.] Crustacean growth. Balkema, The Netherlands.

1986. Population dynamics of the Dungeness crab (*Cancer magister*), 140–153. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 89.

BOTSFORD, L. W., R. D. METHOD, JR., AND W. E. JOHNSTON. 1983. Effort dynamics of the northern California Dungeness crab (*Cancer magister*) fishery. Can J. Fish. Aquat. Sci. 40: 337–346.

BOTSFORD, L. W., AND D. E. WICKHAM. 1975. Correlation of upwelling index and Dungeness crab catch. U.S. Fish. Bull. 73: 901–907.

1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35: 833–843.

CADDY, J. F. 1979a. Long-term trends and evidence for production cycles in the Bay of Fundy scallop fishery. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 97–108.

1979b. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 204–216.

COHEN, J. E., S. W. CHRISTENSEN, AND C. P. GOODYEAR. 1983. A stochastic, age-structured population model of striped bass (*Morone saxatilis*) in the Potomac River. Can J. Fish Aquat. Sci. 40: 2170–2183.

ENNIS, G. P. 1983. The effect of wind direction on the abundance and distribution of decapod crustacean larvae in a Newfoundland nearshore area. Can. Tech., Rep. Fish. Aquat. Sci. 1138: 19 p.

FOGARTY, M. J., AND J. S. IDOINE. 1986. Recruitment dynamics in an American lobster (*Homarus americanus*) population. Can. J. Fish. Aquat. Sci. 43: 2368–2376.

FORD, R. F., B. F. PHILLIPS, AND L. M. JOLL. 1985. Experimental manipulation of population diversity and its affect on growth and mortality of juvenile western rock lobsters, *Panulirus cygnus* George. (Presented at the Lobster Recruitment Workshop, St. Andrews, N.B., July 1985).

GURNEY, W. S. C., S. P. BLYTHE, AND R. M. NISBET. 1980. Nicholson's blowflies revisited. Nature (Lond.) 286: 17–21.

HJORT, J. 1914. Fluctuations in the great fisheries of northern Europe in the light of biological research. Rapp. P.-V. Reun. 20: 1–228.

HORWOOD, J. W. 1983. A general linear theory for the variance of yield from fish stocks. Math. Biosci. 64: 203–225.

1984. The variance and response of biological systems to variability in births and survivals. IMA J. Math. Appl. Med. Biol. 1: 309–323.

HORWOOD, J. W., AND J. G. SHEPHERD. 1981. The sensitivity of age structured populations to environmental variability. Math. Biosci. 57: 59–82.

JOHNSON, D. F. 1982. A comparison of recruitment strategies among Brachyuran crustacean megalopae of the York River, lower Chesapeake Bay and adjacent shelf waters. Ph.D. dissertation, Old Dominion University, Norfolk, VA. 97 p.

JOHNSON, D. F., L. W. BOTSFORD, R. D. METHOD, JR., AND T. C. WAINWRIGHT. 1986. Wind stress and cycles in the Dungeness crab (*Cancer magister*) catch off California, Oregon, and Washington. Can. J. Fish. Aquat. Sci. 43: 838–845.

JOHNSON, D. R., B. S. HESTER, AND J. R. MCCONANGHA. 1984. Studies of a wind mechanism influencing the recruitment of blue crabs on the Middle Atlantic Bight. Cont. Shelf Res. 3: 425–437.

MATHEWS, S. B., AND F. W. OLSON. 1980. Factors affecting Puget Sound coho salmon (*Oncorhynchus kisutch*) runs. Can. J. Fish. Aquat. Sci. 37: 1373–1378.

MAY, R. M., J. R. BEDDINGTON, J. W. HORWOOD, AND J. G. SHEPHERD. 1978. Exploiting natural populations in an uncertain world. Math. Biosc. 42: 219–252.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of western Australia. Fish. Bull. U.S. 80: 475–486.

NELSON, R. N., M. C. INGHAM, AND W. E. SCHAAF. 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish. Bull. U.S. 75: 23–41.

OSTER, G. 1977. Lectures in population dynamics. Lect. Appl. Math. 16: 149–190.

PARRISH, R. H., AND A. D. MACCALL. 1978. Climatic variation and exploitation in the Pacific mackerel fishery. Calif. Dep. Fish Game Bull. 167: 110 p.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster, *In* M. Barnes [ed.] Oceanogr. Mar. Biol. 19: 11–40.

REED, W. J. 1983. Recruitment variability and age structure in harvested animal populations. Math. Biosc. 65: 239–268.

REISH, R. L., R. B. DERISO, D. RUPERT, AND R. J. CARROL. 1985. An investigation of the population dynamics of Atlantic menhaden (*Brevoortia tyrannus*). Can. J. Fish Aquat. Sci. 42 (Suppl. 1): 147–157.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

ROTHLISBERG, P. C. 1982. Vertical migration and its effect on dispersal of penaeid shrimp larvae in the Gulf of Carpentaria, Australia. Fish. Bull. U.S. 80: 541–554.

ROTHLISBERG, P. C., AND C. B. MILLER. 1983. Factors affecting the distribution abundance and survival of *Pandalus jordani* (Decapoda, Pandalidae) larvae off the Oregon coast. Fish. Bull. U.S. 81: 455–472.

ROUGHGARDEN, J., Y. IWASA, AND C. BAXTER. 1985. Demographic theory for an open marine population with space-limited recruitment. Ecology 66: 54–67.

SCARNECCHIA, D. L. 1981. Effects of streamflow and upwelling on yield of wild coho salmon (*Oncorhynchus kisutch*) in Oregon. Can. J. Fish. Aquat. Sci. 38: 471–475.

1984. Climatic and oceanic variations affecting yield of Icelandic stocks of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 41: 917–935.

SCHNUTE, J. 1985. A general theory for analysis of catch and effort data. Can. J. Fish. Aquat. Sci. 42: 414–429.

SHEPHERD, G., M. FOGARTY, AND J. HUGHES. 1985. A stochastic growth model for the American lobster. International Symposium on Age and Growth of Fish, June 1985, Des Moines, IA.

SHEPHERD, J. G. 1982. A versatile new stock and recruitment relationship for fisheries and construction of sustainable yield curves. J. Cons. Int. Explor. Mer 40: 67–75.

STOCKER, M., V. HAIST, AND D. FOURNIER. 1985. Environmental variation and recruitment of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. Can. J. Fish. Aquat. Sci. 42(Suppl. 1): 174–180.

WALTERS, C. J. 1981. Optimum escapements in the face of alternative recruitment hypotheses. Can. J. Fish. Aquat. Sci. 38: 678–689.

# Effect of Assumptions about the Stock–Recruitment Relationship on a Lobster (*Homarus gammarus*) Stock Assessment

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Stock assessment of the European lobster (*Homarus gammarus*) has involved yield per recruit analysis based on the established length cohort methodology of Jones (1974. ICES C.M. 1974/F:33; 1981. FAO Fish. Circ. 734) which assumes that recruitment to the fishery is independent of spawning stock. The Shepherd (1982. J. Cons. Int. Explor. Mer 40: 67–75) model has been used to simulate a range of assumed stock–recruitment relationships, and the resulting sensitivity analysis describes how these affect the relation between yield or biomass and four management variables, namely fishing mortality, minimum carapace length, maximum carapace length, and the capture or noncapture of egg-bearing females. Yield curves show a clear maximum with a marked tendency to stock collapse when fishing effort is high. For the range of simulations considered, the probability of an early recruit failure is greatest for asymptotic stock–recruitment curves, which generate yield curves with maxima at an effort substantially lower than the present level. Only with a highly overcompensatory stock–recruitment curve is there a case for increasing effort to maximise yield, but such a relationship tends to reduce the benefit of increasing minimum carapace length or of setting a maximum carapace length. The model predicts that the assumption made about the stock–recruitment relationship also has a marked effect on the results expected from a ban on the landing of egg-bearing females. Overall the results confirm the unsatisfactory prognosis of the yield per recruit model and emphasise the need to gain an understanding of the biological factors determining the shape of the lobster stock–recruitment curve.

L'évaluation des stocks de homards d'Europe (*Homarus gammarus*) s'est fondée sur une analyse de la production par recrue à partir de la méthode des cohortes de longueur de Jones (1974. ICES C.M. 1974/F : 33; 1981. FAO Fish. Circ. 734) selon laquelle le recrutement pour la pêche est indépendant du stock de géniteurs. Le modèle de Shepherd (1982. J. Cons. Int. Explor. Mer 40 : 67–75) a servi à simuler une série de relations hypothétiques stock–recrutement, et l'analyse de sensibilité qui en résulte décrit la façon dont ces relations affectent le lien entre la production ou la biomasse et quatre variables touchant la gestion : mortalité par pêche, longueur minimum de la carapace, longueur maximum de la carapace et capture ou non capture des femelles grainées. Les courbes de la production montrent un net maximum, avec une tendance marquée à l'effondrement du stock lorsque l'effort de pêche est élevé. Dans la série de simulations considérée, la probabilité d'échec précoce du recrutement est au maximum pour les courbes asymptotiques stock–recrutement, qui donnent des courbes de production présentant des maximums avec un effort nettement inférieur au niveau actuel. C'est seulement en cas de courbe stock–recrutement fortement surcompensatrice qu'il y a lieu d'augmenter l'effort pour maximiser la production, mais cette relation a pour effet de réduire les avantages de l'augmentation de la longueur minimum de la carapace ou de l'établissement d'une longueur maximum. Le modèle prévoit que l'hypothèse émise au sujet de la relation stock–recrutement a aussi un effet marqué sur les résultats que l'on peut attendre d'une interdiction du débarquement des femelles grainées. Dans l'ensemble, les résultats confirment le pronostic défavorable du modèle de la production par recrue et soulignent la nécessité de mieux comprendre les facteurs biologiques qui déterminent la forme de la courbe stock–recrutement chez le homard.

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The fishery for lobster (*Homarus gammarus* L.) in England and Wales is a small boat fishery taking place mainly in coastal waters. The fishery is long established (e.g. see Buckland and Walpole 1877) and since 1900 reported landings have ranged from 300 to 600 t per annum. In the last 15 yr the economic importance of coastal fisheries in England and Wales has increased, bringing increased interest in lobster stock assessment. For example, Hepper (1978) investigated migration, growth, and fishing mortality ($F$) using tagging methods in two English fisheries, whilst length cohort analysis (Jones 1974, 1981) has been used to model the likely effect on yield and biomass per recruit ($Y/R$, $B/R$) of changes in both $F$ and minimum carapace length (MCL) in both the European and English lobster fisheries (Anonymous 1979; Bennett and Edwards 1981).

The application of length-based $Y/R$ analysis to recent data for eight coastal lobster fisheries in England and Wales was summarised by Bannister and Addison (1984) and Bannister (1986). It is shown that for an assumed natural mortality ($M$) of 0.1, present estimates of $F$ in the different fisheries range

from 0.2 to 1.8. In each case, present $F$ exceeds $F_{max}$ (the value giving maximum $Y/R$), $F_{max}$ being variously 25–65% of present $F$. If $F$ is reduced to $F_{max}$ the $Y/R$ model predicts small gains in equilibrium $Y/R$ and moderate to substantial gains in $B/R$. If present $F$ is increased, the model predicts a slight fall in $Y/R$ and $B/R$.

As noted by Bannister (1986), the English lobster assessment is in several respects problematical. Firstly, catch and effort are unreliably reported in some districts so that absolute estimates of stock number derived from a cohort analysis must be viewed with caution. Secondly, deductions drawn from length-based methods may be biased, since size composition may be influenced not only by fishing effort but also by the distribution and behaviour of lobsters in relation to habitat (Howard 1980; Howard and Nunny 1983; Addison 1986). Thirdly, $Y/R$ output is sensitive to the assumption about $M$. With $M = 0.2$, for example, the $Y/R$ model predicts that for some fisheries the present $F$ becomes less than $F_{max}$, such that optimising for $Y/R$ would require an increase in $F$ rather than the decrease predicted for $M = 0.1$. Finally, and most importantly, the $Y/R$ approach takes no account of the possibility of stock collapse at high $F$ values, and so this paper looks at the stock and recruitment problem.

In Europe, previous managers have expressed fears about the possibility of recruitment failure (Anonymous 1979; Bennett and Edwards 1981) but they did not address the problem either analytically or quantitatively. In the English case this is because systematic lobster sampling only began in 1972 and may suffer from the problems noted previously. Tveite and Rørvik (1982) suggested that recruitment is directly proportional to stock for lobsters of the Norwegian–Skaggerak coast. Such an unstable relationship, however, is unlikely to be characteristic of a population without generating an early tendency to collapse as fishing effort increases, and yet in the English fisheries, at least, such a biological collapse has yet to occur despite a prolonged history of exploitation. For Canadian lobster fisheries, $F$ is estimated to have been high for a considerable period (Campbell 1980) but the case for recruitment failure is still not clearly established. Pringle et al. (1983) asserted that recruitment overfishing has occurred, but in at least one fishery, which has been discussed in detail following the advent of the Canso Causeway, the interpretation of the stock–recruitment problem is still far from clear (Dadswell 1979; Robinson 1979; Ennis 1985). These various studies all refer to clawed lobsters. For a spiny lobster, *Panulirus cygnus*, Morgan et al. (1982) concluded that an overcompensatory curve fitted data on spawning stock and puerulus abundance, a result which Ennis (1985) attributed to high fecundity and clear-cut stock identity. However, more recent work suggests that the fit to the data may not be of this form (N. Caputi, Fisheries Department, North Beach, Western Australia, pers. comm.).

Despite the lack of guidance from data, it seems essential for managers to investigate the uncertainty associated with the $Y/R$ approach, and the way we have chosen is by simulation. We have carried out a sensitivity analysis to prescribe the effect on the management viewpoint of applying several different shapes of stock–recruitment curve to the conventional length-based $Y/R$ analysis. We have used the method of Shepherd (1982) who has developed a flexible three-parameter equation capable of expressing varying degrees of density-dependent compensation, which can be coupled to conventional $Y/R$ and $B/R$ output to derive true yield and biomass curves. The simulation approach is adopted because of the lack of historical data and because it provides a clearer view as to how the choice of stock–recruitment relationship may influence management policy.

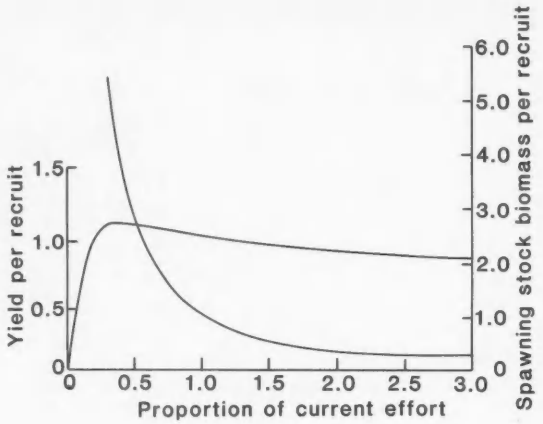


FIG. 1. Yield per recruit and spawning stock biomass per recruit against proportion of current fishing effort for female lobsters in Yorkshire, 1972–80.

## Method

### Yield per Recruit Analysis

For the period 1972–80, size compositions, length–weight, and growth data are available for the eight most important coastal fisheries for lobster in England and Wales, and these were used to estimate $Y/R$ and $B/R$ for a range of exploitation patterns, as described in Bannister (1986) and Bannister and Addison (1984), using the Jones (1974, 1981) length cohort analysis technique. In this paper we consider the results for the Yorkshire coast, where the Jones model predicts that maximum sustainable yield per recruit (MSY/$R$) would be achieved if effort was reduced to approximately 40% of its current value, such that the corresponding $B/R$ would more than double (Fig. 1).

For these data the Jones length cohort analysis provides estimates of current equilibrium spawning stock biomass and the number of recruits to the smallest (80–84 mm) size class. The resulting value for spawning stock biomass is essentially an index of stock equivalent to mean 1972–80 recruitment and does not define absolute stock biomass or egg production. Similarly, recruitment to the fishery is defined by the number of individuals entering the 80–84 mm size class. This may underestimate recruitment, as some recruits will undoubtedly enter the 85–89 mm size class, but since some 85–89 mm lobsters may also have moulted from the 80–84 mm group, and will therefore have been subjected to $F$, the 80–84 mm index has been retained as a fishery-independent index of recruitment. Furthermore, as the model uses a von Bertalanffy continuous growth function, it assumes that all individuals pass through the 80–84 mm size class. It should be noted that only data on female lobsters have been used in the analysis, as including the male population, with its different growth curve and fishing mortality, would further complicate the method without affecting the overall qualitative results.

TABLE 1. Parameters for four stock–recruitment relationships used to describe the Yorkshire lobster fishery (female data only). Equilibrium spawning stock $3.53 \times 10^8$ eggs; equilibrium recruits 68 543.

| | $\alpha$ (recruits per $10^8$ eggs) | $\kappa$ (eggs ($\times 10^{-8}$)) | $\beta$ |
|---|---|---|---|
| 1 | 35 000 | 4.399 | 1.0 |
| 2 | 100 000 | 0.851 | 1.0 |
| 3 | 50 000 | 2.608 | 1.5 |
| 4 | 100 000 | 1.733 | 2.0 |

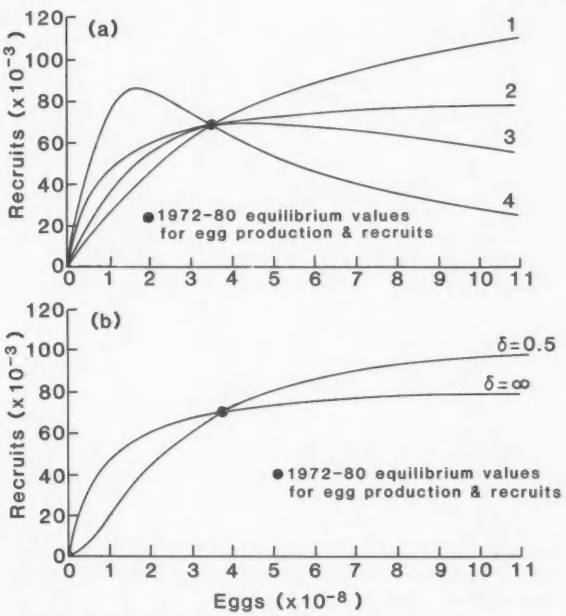


FIG. 2. Theoretical stock–recruitment curves for (a) the four sets of parameter values given in Table 1 and (b) curve 2 of Table 1 either with ($\delta = 0.5$) or without ($\delta = \infty$) a proportional reduction in recruitment at low stock densities.

## Models Including Stock–Recruitment Relationship

The relationship between recruitment to the smallest size class ($R$) and the spawning stock biomass ($B$), expressed as egg production, was described by the model of Maynard Smith and Slatkin (1973) as used by Shepherd (1982):

$$(1) \quad R = \alpha B/[1 + (B/\kappa)^{\beta}]$$

where $\alpha$ represents the slope of the curve at the origin and is a measure of the maximum recruitment per unit biomass, $\beta$ measures the power of the density-dependent effects to compensate for changes in stock sizes, and $\kappa$ is the biomass at which density-dependent effects become dominant. Shepherd (1982) showed that this model is considerably more versatile than the previous stock–recruitment relationships used in a fisheries context by Ricker (1954), Beverton and Holt (1957), and Cushing (1973), while Bellows (1981) has shown that it is the best of a range of such three-parameter models used in the literature to describe analogous density-dependent processes.

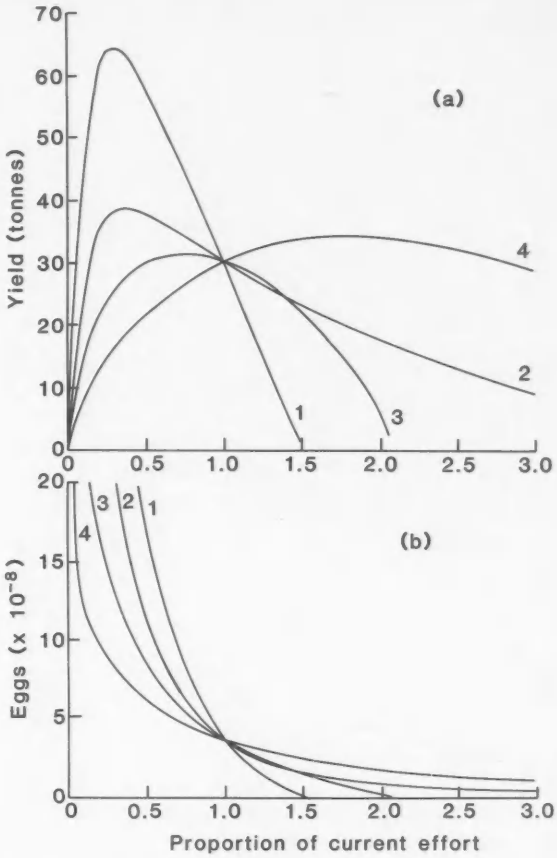


FIG. 3. (a) Yield and (b) eggs against proportion of current fishing effort ($M = 0.1$) for the four stock–recruitment curves of Fig. 2a.

Shepherd's (1982) method involves calculating the biomass corresponding to each level of fishing effort,

$$(2) \quad B = \kappa(\alpha B/R - 1)^{1/\beta},$$

and then using the estimated values for $B/R$ and $Y/R$ to calculate the corresponding values for recruitment ($R$) and hence total yield ($Y$).

The paucity of data concerning stock–recruitment relationships in Crustacea noted by Hancock (1973) still obtains, especially for clawed lobsters, and we cannot predict accurately the expected nature of the relationship from empirical data. Equation 1 has therefore been used to describe a range of relationships which pass through the so-called equilibrium values of recruitment and spawning stock biomass specified for 1972–80 above, according to a series of parameter values chosen following Shepherd's rationale. Table 1 gives four examples of such parameter values for the Yorkshire fishery, assuming $M = 0.1$, and the corresponding curves are shown in Fig. 2a. Curves 1 and 2 are for values of $\beta = 1.0$, assuming that there is "contest" competition (Nicholson 1954) between juvenile stages for available substrate, for example, but $\alpha$ varies between the two curves. Curves 3 and 4 are for values of $\beta > 1.0$, assuming that there is either "scramble" competition (Nicholson 1954) between stages, say for available food resource, or that cannibalism occurs.

### Variation in Parameters and Conditions

Total yield and biomass curves were generated by the above method for four variations in the pattern of exploitation: changes in (1) fishing effort, (2) MCL, (3) maximum carapace length (with a MCL of 80 mm), and (4) MCL with a concurrent ban on the landing of egg-bearing females (berried hens). The predictions of the model for all four variations in exploitation pattern were examined for a range of values of $M$, of fecundity-at-size, and of proportion of berried hens in each size class.

However, changes in some parameters may produce different values of the current equilibrium spawning stock biomass and recruits. A problem may arise here when using, for example, a different value of $M$. To facilitate comparison, therefore, parameter values were scaled so that the current equilibrium biomass and recruit point is always at the same place on the stock–recruitment curve. This will produce a different value of $\kappa$. The ecological interpretation of the parameter $\kappa$ is that at some value of stock biomass, the food resource or suitable holes in the substrate should become scarce for recruits, and hence, density-dependent processes will become significant. This interpretation suggests that this threshold biomass should be the same whatever the level of natural mortality.

### Depensatory Stock–Recruitment Curve

The stock–recruitment curve described by equation 1 is based on the assumption that there is no depensation of the curve at low stock densities. However, for a species such as lobster, which requires both male and female to be in close proximity for the short period when the female is available for mating, it is conceivable that there may be a proportional reduction in the level of recruitment at low stock densities because the probability of a male finding a receptive female may be very low.

A depensatory stock–recruitment curve can be described by the Shepherd (1982) model by the simple addition of a parameter:

$$(3)\quad R = \frac{\alpha B}{1 + (B/\kappa)^{\beta}}\,(1 - \exp(-\delta B))$$

where $\alpha$, $\kappa$, and $\beta$ are as for equation 1 and $\delta$ is a parameter describing the degree of depensation. As $\delta \rightarrow \infty$, the stock–recruitment curve tends to its standard form. However, the addition of a fourth parameter no longer permits a simple rearrangement of the equation to express biomass ($B$) in terms of $B/R$. For the depensatory model, algebraic manipulation gives

$$(4)\quad \frac{1 + (B/\kappa)^{\beta}}{\alpha(1 - \exp(-\delta B))} = \frac{B}{R}.$$

Given the value of $B/R$ for each level of effort, any standard iterative process can be used to solve the above equation for $B$.

Figure 2b shows the depensatory curve described by equation 3 for the same values of $\alpha$ and $\beta$ as given for curve 2, but with $\delta = 0.5$, which produces a value of $\kappa = 1.080$.

## Results

Figure 3 shows the total yield and biomass curves for changes in the level of fishing effort for the Yorkshire fishery when $M = 0.1$. For $\beta = 1.0$ (curves 1 and 2), maximum sustainable yield (MSY) is again at approximately 40% of

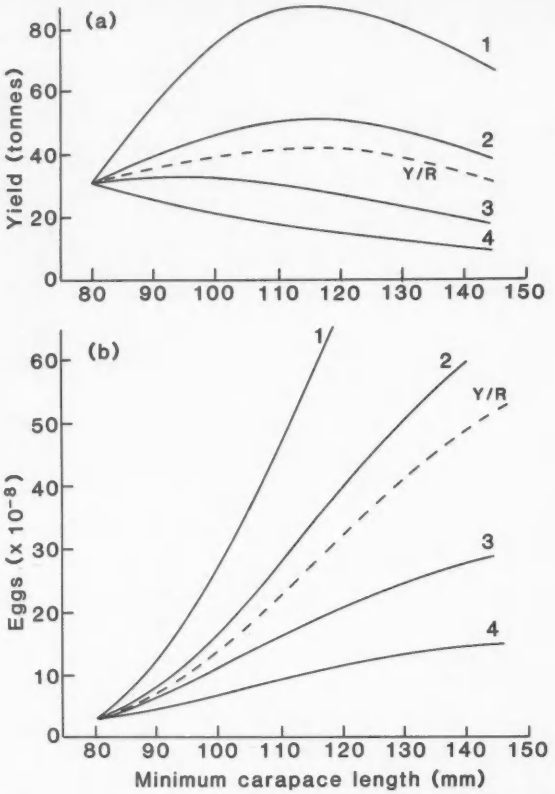


FIG. 4. (a) Yield and (b) eggs against minimum carapace length for the four stock–recruitment curves of Fig. 2a.

current effort, as on the $Y/R$ curve, but because of improved recruitment, yield is substantially higher than when recruitment is assumed to be independent of stock (cf. Fig. 1). However, more importantly, the effect of including such a stock–recruitment relationship in the model is to introduce the possibility of stock collapse if effort is substantially increased, particularly in the case where $\alpha$ is low (curve 1). As $\alpha$ decreases and the density-dependent nature of the relationship is reduced, the relationship approaches one of recruitment being proportional to stock, and the probability of an early recruitment failure is greater. In fact, if recruitment is assumed to be directly proportional to stock biomass, the model is unstable and any perturbation from the current equilibrium point will result in unbounded growth or collapse of the fishery. In contrast, if the assumption about stock and recruitment represents overcompensation for changes in egg production (curves 3 and 4), then the position is less clear. When $\beta = 1.5$ (curve 3), only modest increases in yield would be expected if effort was substantially reduced, but the possibility of stock collapse is introduced at higher effort levels. However, if $\beta = 2.0$ (curve 4), then an increase in effort would initially be beneficial, since stock depletion will first place the stock at the peak of the stock–recruitment curve before a further increase in effort brings the stock into the zone of collapse. Clearly, the true proximity to collapse depends entirely on the scaling generated by the choice of parameters, and in particular on the choice of $\alpha$, but in all cases it is clear that the $Y/R$ ad $B/R$ curves

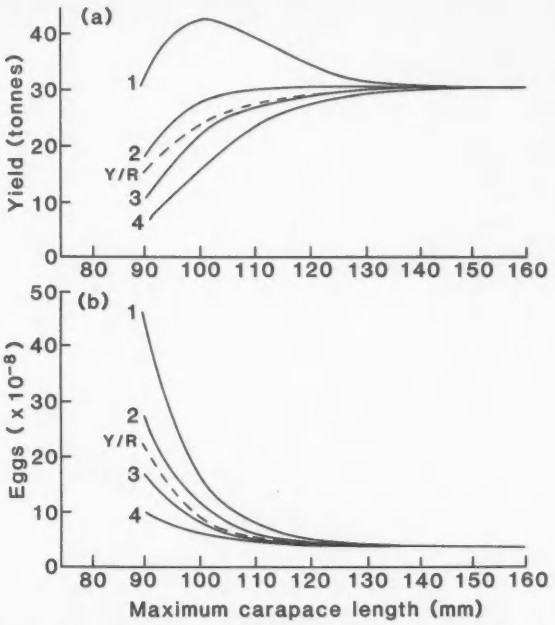


FIG. 5. (a) Yield and (b) eggs against maximum carapace length for the four stock–recruitment curves of Fig. 2a.

(Fig. 1) give a misleading impression of the outcome of sustained high levels of fishing effort.

Figure 4 shows how total yield and biomass vary with minimum size when a relationship between stock and recruitment is assumed. Curves 1 and 2 demonstrate that so long as $\beta = 1.0$ in the stock–recruitment relationship, an increase in minimum size is beneficial, and that the present estimate from $Y/R$ curves is an underestimate of the benefit. Similarly, provided $\beta = 1.0$, the choice of minimum size required to maximize yield is independent of the parameters of the stock–recruitment relationship and is determined predominantly by the level of fishing effort. However, curves 3 and 4 show that when $\beta > 1.0$, an increase in minimum size would actually cause only small increases or a loss in long-term yield, despite small increases in spawning stock biomass.

Figure 5 shows that the introduction of a maximum landing size less than 130 mm (with the minimum size fixed at 80 mm) would reduce $Y/R$, although there would be a significant increase in $B/R$. The introduction of a stock–recruitment relationship may alter this conclusion. For $\beta = 1.0$, it is possible that the introduction of a maximum size may increase both yield and biomass, but only if that limit is considerably below the size of the largest individuals in the fishery. If the stock–recruitment relationship is of an overcompensatory nature (curves 3 and 4), then the introduction of a maximum size would reduce yield. However, a maximum size limit with a concurrent increase in minimum size could provide slightly larger benefits than solely increasing the minimum size (assuming that $\beta$ was not greater than unity), but this would require setting a low maximum size which would involve heavy initial losses to the fishermen. Thus, for management purposes, Fig. 5 suggests that alternative management strategies should be employed in preference to the introduction of a maximum landing size.

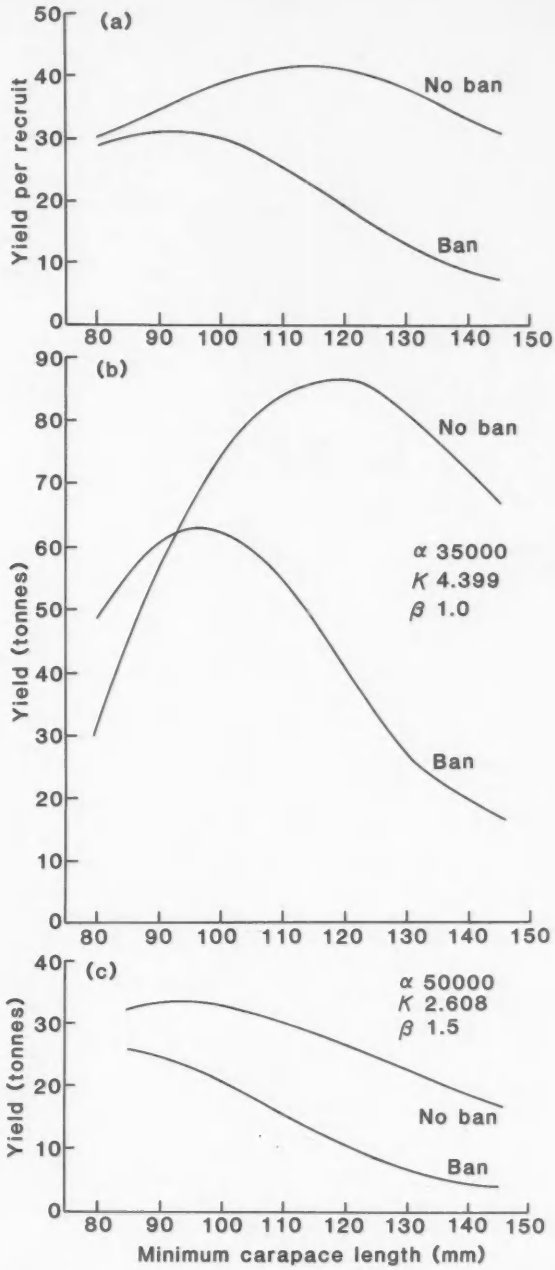


FIG. 6. Effect of a ban on the landing of egg-bearing females on the expected benefits of an increase in minimum carapace length. (a) Yield per recruit against minimum carapace length; (b and c) total yield against minimum carapace length for stock–recruitment curves 1 and 3, respectively, of Fig. 2a.

Figure 6 describes the concurrent effect on long-term yield of both an increase in minimum size and a ban on landing berried hens. Figure 6a is the basic $Y/R$ result. It shows that a ban on landing berried hens reduces long-term $Y/R$ slightly

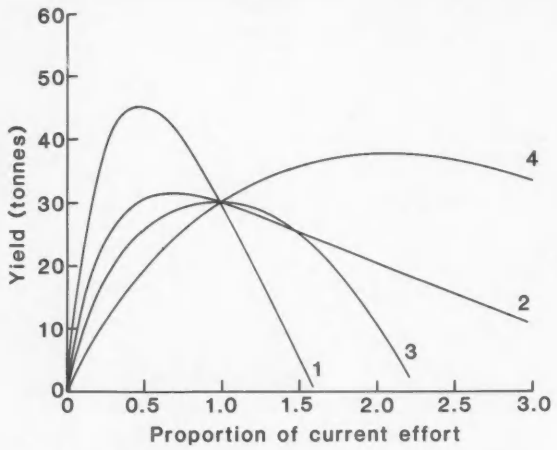


FIG. 7. Yield against proportion of current fishing effort ($M = 0.2$) for the four stock–recruitment curves of Fig. 2a.

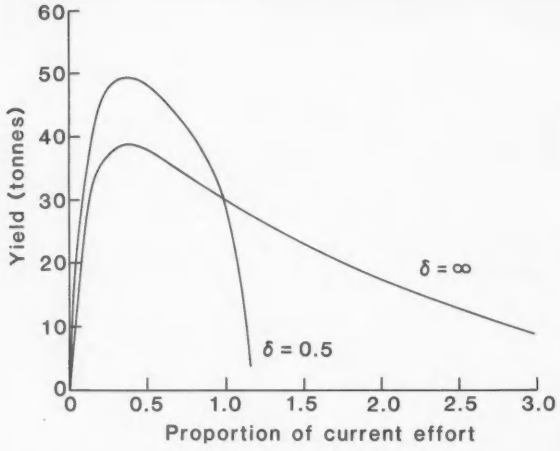


FIG. 8. Yield against proportion of current fishing effort for the two stock–recruitment curves of Fig. 2b.

when there is no change in minimum size and that such a ban would nullify any benefits that might accrue from any increase in minimum size. The effect of introducing a stock–recruitment relationship into the model depends on the nature of that relationship. There may be considerable increases in yield if the relationship is asymptotic ($\beta = 1.0$) and the minimum size is 90 mm or below (Fig. 6b). The minimum size below which a ban is beneficial, and the precise gain in yield, depend on the level of fishing effort and the parameter values describing the stock–recruitment relationship. For $\beta = 1.0$, this gain becomes less marked as $\alpha$ increases, and if there is an overcompensatory relationship, a ban on landing berried hens would reduce long-term yield whatever minimum size was enforced (Fig. 6c). The $Y/R$ analysis is thus misleading when deciding whether or not to introduce a ban on landing berried hens. There may well be circumstances when such a ban could provide significant increases in yield.

Changes in parameters other than those describing the stock–recruitment relationship, such as the level of natural mortality, the fecundity-at-size, and the proportion of berried hens in each size class, did not greatly affect the qualitative predictions of the model. Although specific quantitative predictions such as the absolute value of the maximum yield, or the point of collapse of the fishery, will be determined by the above parameters, the general shape of the yield and biomass curves is more robust to changes in these parameters. For example, Fig. 7 shows the total yield curves for changes in fishing effort for the stock–recruitment curves of Fig. 2a when $M = 0.2$. These predicted curves are very similar to those described by Fig. 3a where $M = 0.1$. This is in contrast with the sensitivity of the standard $Y/R$ model to changes in $M$ that was outlined in the introduction.

The effect of introducing a depensatory stock–recruitment curve into the model is described in Fig. 8. The model predicts that the maximum yield is higher, as expected, but that the point of recruitment collapse is at less than 20% above the present level of effort. The increased likelihood of collapse with this model, which assumes a proportional reduction in the level of recruitment at low stock densities, can be explained by recalling that the stock will collapse if the biomass per recruit falls below the critical value of the reciprocal of the slope of the stock–recruitment relationship at the origin (Shepherd 1982). Clearly, the implications for management of this particular assumption about the stock–recruitment relationship are very serious.

## Discussion

In attempting to study stock and recruitment, two problems are frequently encountered. Firstly, data my be nonexistent or poor, as with *Homarus gammarus*, and secondly, where there are data, it is usually difficult to distinguish statistically between the fit of different models. The temptation is then to retreat to the $Y/R$ approach and to miss the essential point that, whatever the relationship, stock may collapse at high $F$. Shepherd (1982) developed his model in order to combine existing data, graphical estimation, and biological principles to establish a stock–recruitment curve for a particular set of observations. Our objective has not been to define the stock–recruitment curve which actually applies to lobster data, but to use several simulations to see if it is possible to generalise about the management position for different shapes of curve irrespective of the precise parameter values which may actually apply.

Caution is necessary in drawing conclusions from a limited set of simulations, but some important general points emerge. Considering first the relation between yield and effort, there is a clear-cut maximum in the yield curve, with a marked tendency for stock to collapse at high effort for all parameter combinations. In the cases studied the model predicts collapse at an effort of from 1 to 3 times the present level, and only when there is a strong degree of overcompensation is there any indication that an increase in effort would increase yield. Results suggest that it is the parameter $\beta$ which defines the level of $F$ giving maximum yield (i.e. $F_{max}$). Within each choice of $\beta$, changes in the parameter $\alpha$ do not appear to affect $F_{max}$, but $\alpha$ does affect the absolute yield maximum, the predicted collapse point, and the rate of approach to it. For $\beta = 1.0$, and several choices of $\alpha$, $F_{max}$ is approximately the same as defined by the $Y/R$ model for $M = 0.1$. If the objective is to maximise yield,

and if there are gounds for assuming that $\beta = 1.0$, then the $Y/R$ model for $M = 0.1$ may be sufficient to define $F_{max}$ and $\alpha$ may not need to be investigated. Present results also show that the ambiguity noted in the introduction concerning the effect of $M$ on the shape of the $Y/R$ curve is removed by including a stock–recruitment function. Overall, the probability of an early recruit failure increases as both $\beta$ decreases and, within each $\beta$, as $\alpha$ decreases. This has a twofold management implication. Firstly, unless there is positive evidence that the stock–recruitment relationship is overcompensatory (curve 4), the most realistic strategy for the prevention of stock collapse is to prevent any further increase in effort. Secondly, the most realistic general strategy for maximising yield would be to reduce $F$ to approximately $F_{max}$ on the $Y/R$ curve for $M = 0.1$.

For the other management variables, results show that the likely yield benefits from raising MCL or setting a maximum carapace length will change as both $\alpha$ and $\beta$ change, but the main observation is that if $\beta \leq 1.0$, yield benefits exceed those predicted by the $Y/R$ model, but if $\beta > 1.0$, the benefits are less than for the $Y/R$ model. For a ban on the landing of egg-bearing females, a previous study using the $Y/R$ approach pointed to the potential increase in egg production but suggested that the increase in yield would be negligible (Bennett and Edwards 1981). This study shows that the result for yield depends significantly on the assumption made about the stock–recruitment curve. A ban on the landing of egg-bearing females is currently absent from the national lobster legislation in Britain.

Although further simulations are required to test the various conclusions, the preliminary results are that if the management objective is to maximise yield it is more important to know $\beta$ than to know $\alpha$. If the concern is to explore how far $F$ can increase without endangering stock, then both $\beta$ and $\alpha$ must be known, and $\alpha$ is particularly important. In fitting the model to data, the estimate obtained for $\alpha$ depends very much on the range of stock size for which data are available. If stock is still well above the likely collapse point, the graphical estimation of $\alpha$ as the slope of the line drawn from the origin through the left-hand margin of the data set (Shepherd 1982) will be conservative and "fail-safe." Qualitatively, however, very similar stock–recruitment curves can be described by quite different parameter values. Quite unreasonable conclusions about the degree of overcompensation in the process, and hence about the underlying biology, could arise from some statistical quirk in parameter estimation. It may be preferable therefore to use biological information to fix either $\alpha$ or $\beta$, or indeed $\kappa$. In fact, $\beta$ is a parameter which can only realistically be deduced by studying the characteristics of the compensatory mortality process. To favour $\beta$ values in excess of 1.5, we should find field evidence of overcompensatory mortality in the planktonic or benthic phase, whether due to cannibalism, aggregation of predators, or extreme resource or space limitation, whilst for lower $\beta$ values we should be looking for some threshold effect in resource or spatial limitation. Stock–recruitment processes with high $\beta$ values should also tend to produce cyclical behaviour under perturbation (Fogarty and Idoine 1986). From the purely management viewpoint the total yield curves are governed more by the shape of the stock–recruitment curve than by the particular values of its parameters. As noted in the introduction, in the few examples available the analyses of both clawed and spiny lobster stock and recruitment data are inconclusive. As with fish, the need therefore is for more specific studies aimed at describing and understanding prerecruit regulatory processes.

## References


ADDISON, J. T. 1986. Density-dependent mortality and the relationship between size composition and fishing effort in lobster populations. Can. J. Fish. Aquat. Sci. 43: 2360–2367.

ANONYMOUS. 1979. Report of the *Homarus* working group. ICES C.M. 1979/K:8. (Mimeo.)

BANNISTER, R. C. A. 1986. Assessment and population dynamics of commercially exploited shellfish in England and Wales, p. 182–194. *In* G. S. Jamieson and N. Bourne [ed.] North Pacific Workshop on stock assessment and management of invertebrates. Can. Spec. Publ. Fish. Aquat. Sci. 92.

BANNISTER, R. C. A., AND J. T. ADDISON. 1984. The effect on yield and biomass per recruit of changes in fishing mortality and size at first capture in the fisheries for lobster, *Homarus gammarus* L., in England and Wales. ICES C.M. 1984/K:10. (Mimeo.)

BELLOWS, T. S. 1981. The descriptive properties of some models for density dependence. J. Anim. Ecol. 50: 139–156.

BENNETT, D. B., AND E. EDWARDS. 1981. Should we ban the berried lobster? ICES C.M. 1981/K:11. (Mimeo.)

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. Lond. Ser. II, 19: 533 p.

BUCKLAND, F., AND S. WALPOLE. 1877. Reports on the crab and lobster fisheries of England and Wales. H.M.S.O., London.

CAMPBELL, A. 1980. A review of mortality estimates of lobster populations in the Canadian maritimes. Can. Tech. Rep. Fish. Aquat. Sci. 932: 27–36.

CUSHING, D. H. 1973. The dependence of recruitment on parent stock. J. Fish. Res. Board Can. 30: 1965–1976.

DADSWELL, M. J. 1979. A review of the decline in lobster (*Homarus americanus*) landings in Chedabucto Bay between 1956 and 1977 with an hypothesis for a possible effect by the Canso Causeway on the recruitment mechanism of eastern Nova Scotian lobster stocks. Fish. Mar. Serv. Tech. Rep. 834.

ENNIS, G. P. 1985. An assessment of the impact of size limit and exploitation rate changes on egg production in a Newfoundland lobster population. N. Am. J. Fish. Man. 5: 86–90.

FOGARTY, M. J., AND J. S. IDOINE. 1986. Recruitment dynamics in an American lobster (*Homarus americanus*) population. Can. J. Fish. Aquat. Sci. 43: 2368–2376.

HANCOCK, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P.-V. Réun. Cons. Int. Explor. Mer 164: 113–131.

HEPPER, B. T. 1978. Population dynamics of the lobster *Homarus gammarus* (L.) off the coasts of England. Fish. Res. Tech. Rep. MAFF Dir. Fish Res. Lowestoft 41: 29 p.

HOWARD, A. E. 1980. Substrate controls on the size composition of lobster (*Homarus gammarus* L.) populations. J. Cons. Int. Explor. Mer 39: 130–133.

HOWARD, A. E., AND R. S. NUNNY. 1983. Effects of near bed current speeds on the distribution and behaviour of the lobster, *Homarus gammarus* (L.). J. Exp. Mar. Biol. Ecol. 71: 21–42.

JONES, R. 1974. Assessing the long term effects of changes in fishing effort and mesh size from length composition data. ICES C.M. 1974/F:33. (Mimeo.)

1981. The use of length composition data in fish stock assessments (with notes on VPA and cohort analysis). FAO Fish. Circ. 734: 55 p.

MAYNARD SMITH, J., AND M. SLATKIN. 1973. The stability of predator–prey systems. Ecology 54: 384–391.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of Western Australia. Fish. Bull. 80: 475–486.

NICHOLSON, A. J. 1954. An outline of the dynamics of animal populations. Aust. J. Zool. 2: 9–65.

PRINGLE, J. D., D. G. ROBINSON, G. P. ENNIS, AND P. DUBÉ. 1983. An overview of the management of the lobster fishery in Atlantic Canada. Can. MS Rep. Fish. Aquat. Sci. 1701: 103 p.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

ROBINSON, D. G. 1979. Consideration of the lobster (*Homarus americanus*) recruitment overfishing hypothesis; with special reference to Canso Causeway. Fish. Mar. Serv. Tech. Rep. 834: 77–99.

SHEPHERD, J. G. 1982. A versatile new stock–recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. Int. Explor. Mer 40: 67–75.

TVEITE, S., AND C. J. RØRVIK. 1982. A stock assessment of lobster (*Homarus gammarus*) on the Norwegian Skagerrak coast. ICES C.M. 1982/K:7. (Mimeo.)

# Density-Dependent Mortality and the Relationship between Size Composition and Fishing Effort in Lobster Populations

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Addison, J. T. 1986. Density-dependent mortality and the relationship between size composition and fishing effort in lobster populations. Can. J. Fish. Aquat. Sci. 43: 2360–2367.

Examination of time series data from lobster fisheries shows that although in some cases fishing mortality (estimated from size composition data) is directly related to fishing effort, that of many stocks remains relatively unchanged despite changes in the pattern of exploitation. This suggests that conventional stock assessment models used for finfish populations may not be adequate for lobster populations. A model is described which incorporates into a standard yield per recruit model density-dependent mortality in large lobsters due to limited availability of suitable holes in the substrate. The model predicts that size composition may change little with changes in fishing effort, and it is shown that current stock assessment methods may fail to detect those changes. The underlying assumptions of current methods are undermined further by the possible delay of moulting of lobsters that cannot find shelters.

L'examen des séries chronologiques de données sur les pêches du homard montre que, si dans certains cas la mortalité par pêche (estimée à partir des données sur la composition par taille) est directement en rapport avec l'effort de pêche, celle de nombreux stocks reste relativement stable malgré des modifications du mode d'exploitation. On peut en déduire que les modèles classiques d'évaluation des stocks utilisés pour les populations de poissons peuvent ne pas convenir à celles de homards. Nous décrivons un modèle qui intègre à un modèle standard de la production par recrue la mortalité dépendante de la densité chez les homards de grande taille à cause du manque d'abris convenables dans le substrat. Le modèle prévoit que la composition par taille peut ne changer que très peu lorsque l'effort de pêche se modifie, et il apparaît que les méthodes actuelles d'évaluation des stocks ne permettent pas de repérer ces modifications. Les hypothèses qui sous-tendent les méthodes actuelles sont encore ébranlées par le fait que la mue des homards peut être retardée lorsqu'ils ne trouvent pas d'abris.

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Stock assessment of crustacean populations usually has involved some standard dynamic pool model based on the assumption that recruitment to the fishery is independent of the spawning stock (e.g. Anonymous 1979; Fogarty 1980; Ennis 1980; Bannister and Addison 1984; Campbell 1985). These models generally assume that recruitment from one size class to the next within the fishery is based entirely on the growth rate, the level of fishing mortality, and the natural mortality occurring in each size class. Thus, these standard yield per recruit analyses assume that the size composition of the catch is an index of the level of fishing effort and that the size composition responds to changes in the pattern of exploitation in the same manner as finfish populations.

The simplest validation of such models is to examine time series data on catch, effort, catch-per-unit-effort, and the level of fishing mortality (calculated from size composition data) from a range of fisheries. Validations from lobster fisheries are conflicting. In some fisheries there is a clear relationship between fishing mortality and fishing effort, but in others the size composition of the catch appears to have remained relatively unchanged over a considerable period of time despite marked changes in fishing effort.

Skud (1969) noted that the size composition of catches of *Homarus americanus* from the offshore canyons of the American fishery had shifted towards smaller individuals between surveys in 1956 and 1965–67, and he suggested that this was due to an increase in fishing effort. Fogarty et al. (1982) undertook a more detailed assessment of the offshore fishery of Georges Bank and southern New England and split the length frequency data into two periods representing the initial development of the fishery (1966–71) and a period of increased exploitation (1972–80). Cohort analysis of the length frequency data clearly shows that fishing mortality was very much higher in both areas of the fishery during the period of heavy exploitation than during the initial period. However, this change in size composition may be partially attributable to a transition from a trawl-based fishery to a trap fishery.

Tveite and Rørvik (1982) provided comprehensive details of catch, effort, catch-per-unit-effort, and size composition data from the Norwegian fishery for *Homarus gammarus* in the Skagerrak. Fishing effort and fishing mortality (estimated from cohort analysis) were relatively stable from 1950 to 1962, and effort then dropped dramatically from 1962 to 1980. There was no drop in fishing mortality until 1974. Catch, catch-per-unit-effort, and stock biomass (estimated from cohort analysis) all declined steadily throughout 1950–80. Tveite and Rørvik (1982) suggested that the lack of correlation between fishing mortality and effort may be due to poor reporting of catch and effort statistics and the time delay between changes in effort and the change in size composition. Nevertheless, there were considerable changes in catch, effort, and catch-per-unit-effort between 1950 and 1974 when the size composition of the catch remained relatively stable.

The size composition of *Homarus gammarus* caught in the

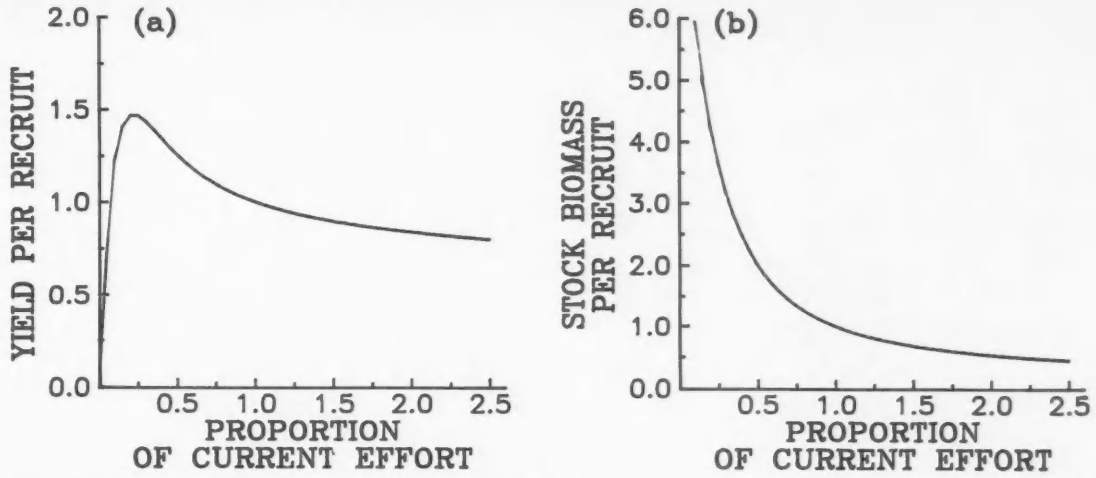


FIG. 1. (a) Yield and (b) stock biomass per recruit against proportion of current fishing effort for *Homarus gammarus* off the Yorkshire coast of England.

Cornwall fishery in southwest England has changed little since the 1950s. Cohort analysis of data published by Hepper (1978) provides a value of fishing mortality of 0.40 for 1956–60 compared with a value of 0.34 for 1972–80 (Bannister and Addison 1984), yet fishing effort has increased considerably over this period of time.

Robinson (1979) provided good evidence from fishery experimental grounds off Miminegash, Prince Edward Island, that *Homarus americanus* populations behave in the expected manner when fishing effort is increased. The proportion of market-size (>81 mm carapace length) lobsters in the catch declined linearly with increasing numbers of trap hauls in the fishery.

Pezzack and Duggan (1983) found that the size composition of catches of *Homarus americanus* in the Canadian offshore fishery on northeastern Georges Bank and Browns Bank had changed little between 1972 and 1980. Although fishing effort had remained fairly steady on Georges Bank during that period, it had increased considerably on Browns Bank.

The lack of correlation between fishing effort and fishing mortality (estimated from size composition data) may be due to problems of collation and interpretation of effort and size composition data (see Discussion). The examples cited may lead also to a reappraisal of the underlying assumptions of the models used for lobster stock assessment. It must be assumed that the level of fishing effort to some extent determines the size composition of the population. Other population processes which might influence the size composition should be identified and consequently incorporated into the stock assessment models.

Density-dependent natural mortality of large lobsters due to substrate limitation is one feature that may be important in the population dynamics of the lobster (Howard 1980; Howard and Nunny 1983). Howard (1980) examined the size composition of the catch and the nature of the substrate in different areas off the east coast of England and proposed that the habitat is limiting in the Norfolk fishery because the solid cover of appropriate size, which is essential to the survival of lobsters, is not present. The hypothesis was tested in flume tanks and the results suggested that habitat limitation operated because lobsters must avoid currents created by tidal and wave action and that this limitation is size selective. Thus, it would seem quite reasonable to assume that density-dependent mortality of large lobsters must occur in some fisheries.

The object of this study was to incorporate density-dependent natural mortality of large individuals into a standard yield per recruit model and to consider the consequences of such mortality on the relationship between size composition and fishing effort.

## Predictions of Standard Yield per Recruit Model

The limitations of the standard yield per recruit models are exposed when one considers the predictions from the model for changes in fishing effort based on catch-at-length data. Figure 1 shows a typical yield and biomass per recruit curve for the lobster fishery off the east coast of England using the length cohort analysis technique of Jones (1974, 1981). To maximize the yield per recruit from the fishery, fishing effort should be reduced to about 25% of its present level with a corresponding increase in stock biomass of approximately 300%. These predictions are based on the assumption that the substrate is capable of supporting an unlimited number of individuals of any size class. Figure 2 shows the size composition of the catch at present and the size composition of the population predicted by length cohort analysis. It also shows the predicted size composition of the catch and population when yield per recruit is at its maximum. At this level of fishing mortality ($F_{max}$) the population contains at least 10 times the number of individuals above 110 mm carapace length than at present. In contrast, diving studies off the north Norfolk coast imply that the substrate might support only 2–3 times the present number of large lobsters. As the presence of large lobsters in the catch is the reason for the peak in the yield per recruit curve, it suggests that to manage the fishery to reach $F_{max}$ based on a standard yield per recruit model may be misguided.

## Model Including Density-Dependent Mortality

The model is based on following a cohort of recruits through

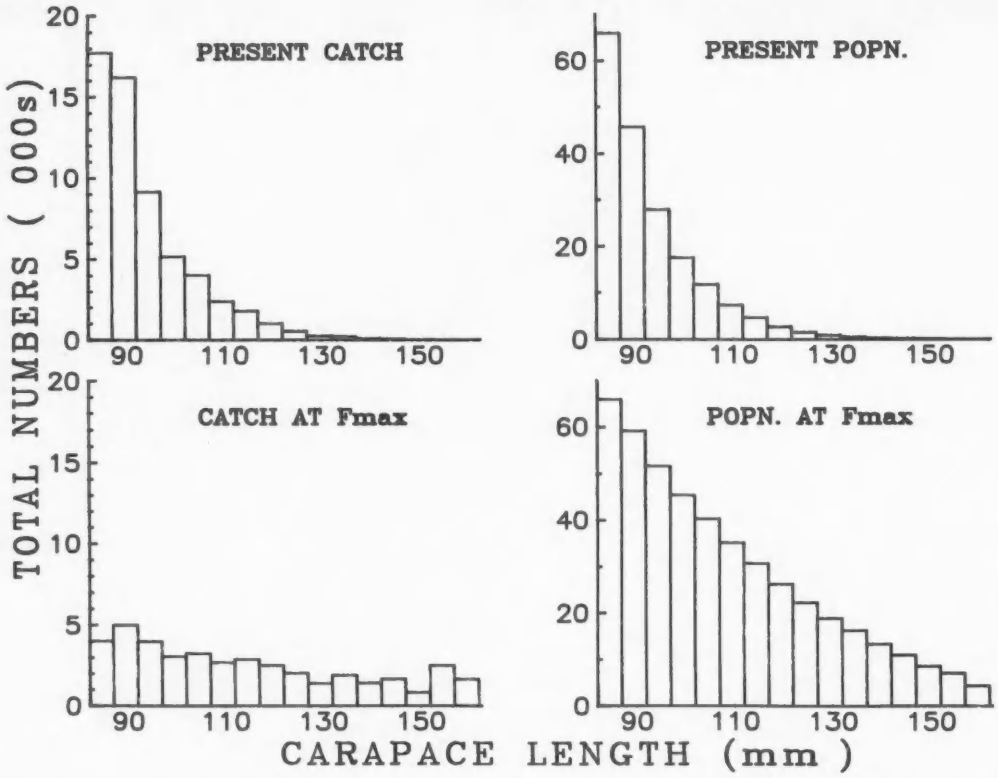


FIG. 2. Size composition of catch and predicted size composition of present population and future catch and population at $F_{max}$. (Estimates of fishing mortality vary with size, so the catch at $F_{max}$ is not monotonically decreasing.)

their life history. The change in population numbers ($N$) from the time that individuals enter a size class ($t$) to the time they leave it ($t + \Delta t$) is given by

$$(1) \quad N_{t+\Delta t} = N_t[1 - \exp(-(F + M)\Delta t)]$$

where $\Delta t$ is the time taken to pass through the size class, $F$ is the coefficient of fishing mortality, and $M$ is the coefficient of natural mortality. The catch during the time interval $\Delta t$ is given by

$$(2) \quad C = \frac{F}{F + M}[1 - \exp(-(F + M)\Delta t)].$$

The model assumes that at time $t + \Delta t$ all individuals moult and recruit to the next size class, but that the proportion that reach the next size class is determined by the density of individuals because of the limited availability of suitable holes in the substrate. Competition for available holes occurs only between individuals of the same size class. Hence, the numbers entering the next size class ($R$) is given by

$$(3) \quad R = N_t[1 - \exp(-(F + M)\Delta t)] \cdot S(N_{t+\Delta t}) = N_{t+\Delta t} \cdot S(N_{t+\Delta t})$$

where $S$ is some density-dependent function. The model assumes that both natural and fishing mortality occur continuously during the intermoult period, but that density-dependent recruitment to the next size class involves further mortality which occurs instantaneously. This seems a reasonable assumption on the basis that the time taken to find a suitable refuge and moult is negligible in comparison with the intermoult period. The model's assumptions are considered more fully in the later discussion.

A versatile density-dependent function for equation 3 is that of Shepherd (1982). The model is of the form

$$(4) \quad S(N) = \frac{\lambda}{1 + (N/D)^{\beta}}$$

where $S(N)$ is the proportion of $N$ that enters next size class, $N$ is the number of individuals reaching the end of the previous size class, $\lambda$ is the density-independent survival of individuals, $D$ is the threshold density, and $\beta$ is the degree of compensation.

## Example of the Model

In this example, four size classes have been used to emphasize the effect on population dynamics that the introduction of density-dependent mortality can have on the standard yield per recruit model. The 10-mm size classes with lower limits of 80, 90, 100, and 110 mm carapace length were chosen because this covers the range of sizes found in the commercial catch of the Norfolk fishery where substrate limitation is thought to occur. These size classes are equivalent to the approximate growth increment of 10 mm carapace length per moult that is observed over this size range (Hepper 1967). The intermoult periods (values of $\Delta t$) are calculated from the fitting of a Ford–Walford plot based on moult increment data using the anniver-

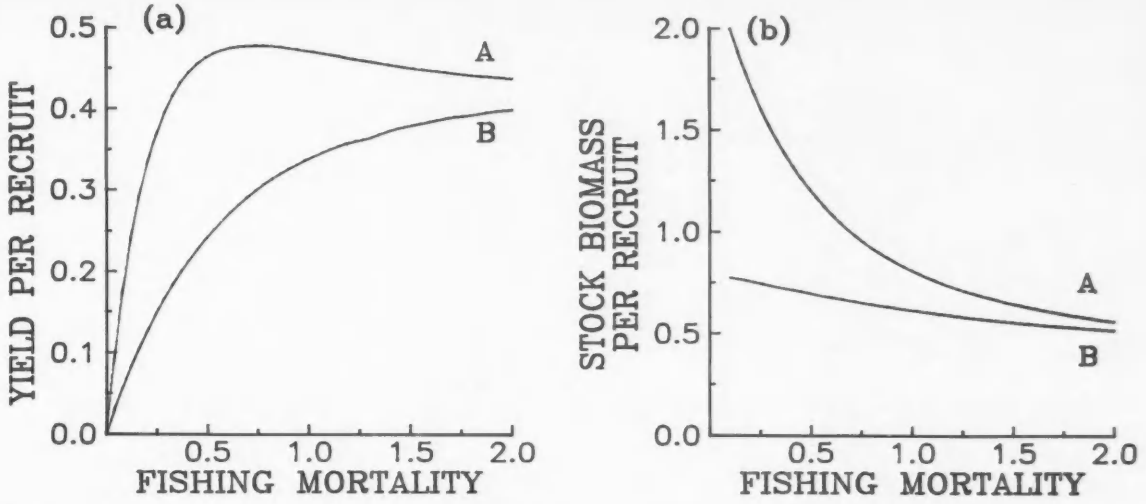


FIG. 3. Comparison of (a) yield and (b) biomass per recruit for standard model (A) and model with density-dependent recruitment (B).

TABLE 1. Intermoult period ($\Delta t$), fishing mortality ($F$), and recruitment maximum ($D$) for model B.

| Size class (mm) | $\Delta t$ (yr) | $F$ (as proportion of $F_{80-89}$) | $D$ |
|---|---|---|---|
| 80–89 | 0.73 | 1.0 | — |
| 90–99 | 0.87 | 1.33 | 5000 |
| 100–109 | 1.06 | 1.17 | 3000 |
| 110–119 | 1.37 | 1.0 | 2000 |

sary method, and from the von Bertalanffy growth equation

$$(5)\quad \Delta t = \frac{1}{K} ln\left(\frac{L_\infty - L_1}{L_\infty - L_2}\right),$$

where $L_\infty$ is the maximum size, $L_1$ and $L_2$ are the lower and upper limits of the size range, and $K$ is the growth parameter. (Values of $\Delta t$ can, of course, be set using any form of moult increment data.)

The model assumes that there are 10 000 recruits to the 80–89 mm size class and a mortality rate ($M$) of 0.1. Fishing mortality ($F$) is not constant with size but follows the pattern given in Table 1, along with values of $\Delta t$ for the respective size classes. Assuming that there is no density-independent mortality during the moulting stage (but see later discussion), and that "contest" competition (Nicholson 1954) for available holes occurs (i.e. $\beta = 1.0$), then equation 4 reduces to

$$(6)\quad S(N) = \frac{1}{1 + N/D}$$

which provides the interpretation of the parameter $D$ as the maximum number of individuals of the next size class that the substrate can support. In this example the recruitment limits to each size class given in Table 1 have been set.

## Predictions of the Model

The model has been used to generate yield and biomass per recruit curves with (curve B) and without (curve A) density-dependent mortality during recruitment to large size classes (Fig. 3). The results for model B suggest that, providing there is no danger of recruitment failure, i.e. that the spawning stock biomass does not drop below the critical level at which recruitment fails, the optimal fishing strategy always would be to increase fishing effort and thus catch all individuals as soon as possible after their recruitment to the fishery. This is in direct contrast with the predictions of the standard model (A), which assumes constant low $M$, where a reduction in effort is required to achieve maximum sustainable yield. For the model incorporating density-dependent recruitment to large size classes, such a reduction in effort would generate a small increase in biomass per recruit but a significant loss in yield per recruit. The predictions of model B are similar to those from the standard model run with a high level of natural mortality.

Figure 4 shows the size composition of the catches that the two models predict for the three levels of fishing effort, $F_{80-89} = 0.3$, 0.6 and 1.2. The most striking features of these size compositions are that, as expected, the model including density-dependent recruitment (model B) predicts size compositions that would normally suggest much higher levels of $F$ than are present and that changes in effort predict relatively small changes in size composition. The value of fishing mortality that would normally be associated with such size compositions can be calculated simply by looking at the population numbers at size and assuming

$$(7)\quad Z = \frac{1}{\Delta t} \ln\left(\frac{N_{L+10}}{N_L}\right)$$

where $Z = F + M$ and $N_L$ are the population numbers of size class with lower limit $L$ (millimetres). In a standard stock assessment, however, we do not know the population numbers-at-size or the array of fishing mortality-at-size. Usually, only the catch-at-size is known. Therefore, the standard technique of Jones' (1974, 1981) length cohort analysis has been used to examine the size composition, assuming constant natural mortality rate, and its predictions compared with the preset parameter values used to generate size compositions from the simulation model.

Two approaches were made. Firstly, the Jones method was

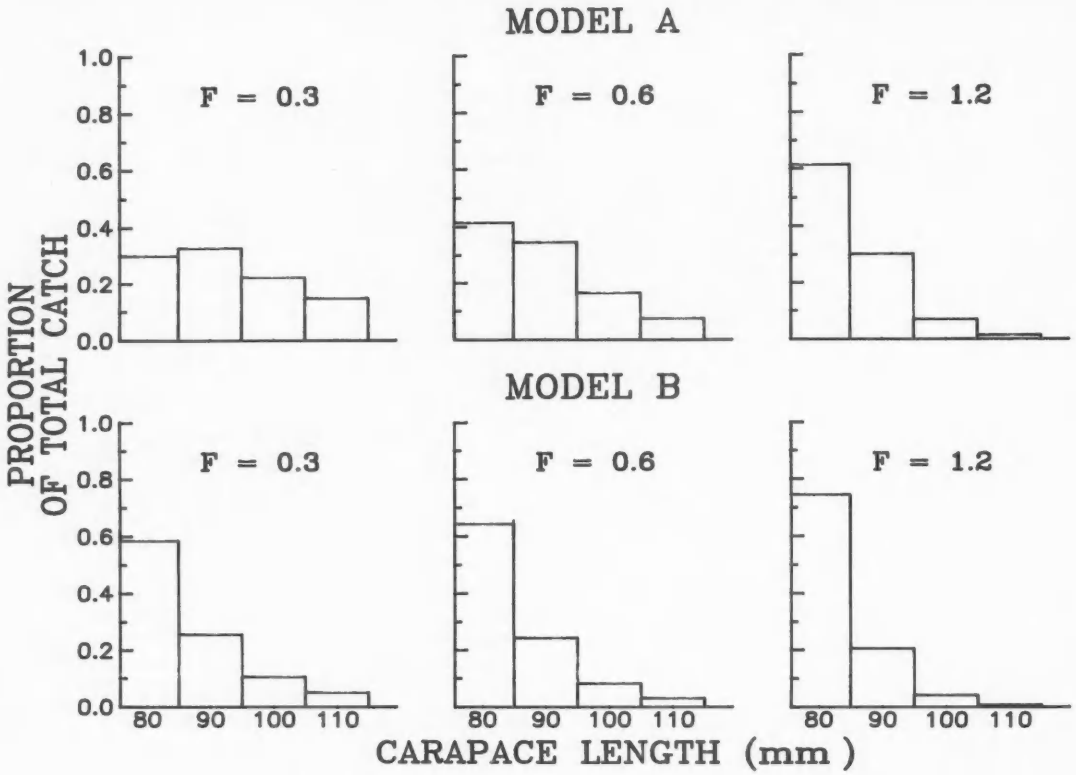


FIG. 4. Size composition of catch predicted by models A and B for three levels of fishing mortality.

used to analyse the size compositions of Fig. 4 (model B). The first point to note is that, assuming $M = 0.1$, this method calculates $F \approx 1.25$ for the size composition predicted by the density-dependent model (model B) when $F_{80-89} = 0.6$. In other words, it apportions the total mortality ($Z$) in a different way than model B. However, the most important point is that for a size composition generated by model B for a 50% reduction in $F$ ($F_{80-89} = 0.3$), the Jones model predicts a value for $F$ of 1.03, which is equivalent to a reduction of only 18%. Similarly, a size composition generated by model B for a doubling of $F$ ($F_{80-89} = 1.2$) suggests an increase in $F$ of only 40% when analysed using the Jones method.

A second approach would be to take the initial equilibrium size composition at $F_{80-89} = 0.6$ from Fig. 4 (model B) as the catch-at-length data and use Jones' (1981) method for calculating changes in yield per recruit for a change in exploitation pattern. For each size class:

$$(8)\quad \text{New catch} = \text{Old catch} \times \frac{S_2}{S_1} \times \frac{\text{new effort}}{\text{old effort}} \times \exp(\phi)$$

where $S_1$ and $S_2$ are old and new selection coefficients and $\phi$ is the sum of changes in mortality in all previous size classes:

$$(9)\quad \phi = \sum_{i=1}^{L-1} [(F_1 - F_2)\Delta t_i] + \left(\frac{F_1 - F_2}{2}\right)\Delta t_L$$

where $L$ is the size class under consideration.

Figure 5 shows the predicted size compositions following a 50% reduction and 100% increase in fishing effort from the Jones model. Comparison of Fig. 5 with Fig. 4 (model B) shows that the Jones model overestimates changes to the size composition when changes in fishing effort occur. There are two reasons for this. Firstly, the Jones method greatly overestimates $F$ in the equilibrium position and therefore a 50% reduction in effort still assumes a much higher $F$ than in model B, and similarly a doubling of effort in the Jones method pushes $F$ to a high level compared with that for model B. Table 2 shows the effective levels of fishing mortality that the two methods assume. The second reason is, of course, that the density-dependent mortality in large lobsters dampens the effect of the change in effort in model B.

TABLE 2. Values of fishing mortality estimated from Fig. 5 (Jones model) and for model B ($F_{80-89}$).

| Effort | Jones model | Model B |
|---|---|---|
| 50% reduction | 0.625 | 0.3 |
| Current | 1.25 | 0.6 |
| 100% increase | 2.50 | 1.2 |

Variation of Parameters

As most of the natural mortality that occurs throughout the year is likely to occur during the moult stage when the animal is most vulnerable, it would be more realistic to use values of $M < 0.1$ and perhaps set the density-independent parameter $\lambda$ in equation 4 equal to less than unity. However, this alters the interpretation of the parameter $D$ and causes no significant

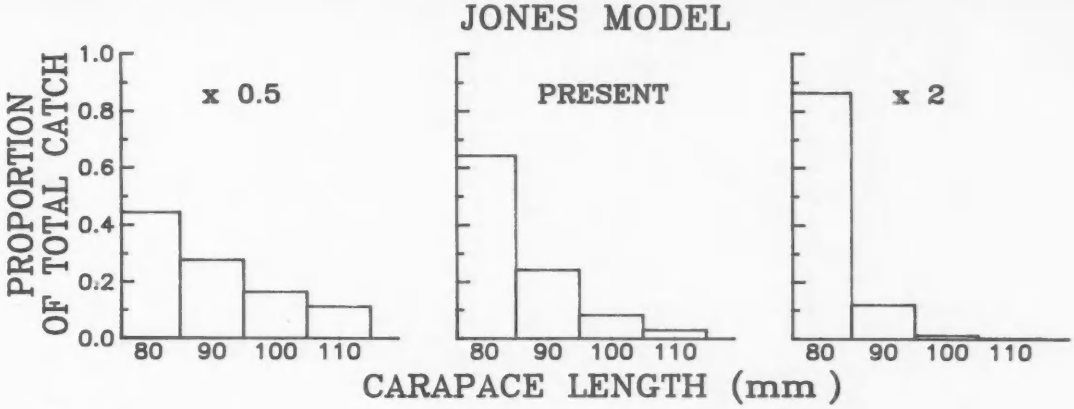


FIG. 5. Prediction of size compositions of catch for the Jones model for a 50% reduction and 100% increase in effort.

TABLE 3. Intermoult period ($\Delta t$), fishing mortality ($F$), and recruitment maximum ($D$) for model predictions of Fig. 6a.

| Size class (mm) | $\Delta t$ (yr) | $F$ (not size dependent) | $D$ |
|---|---|---|---|
| 80–89 | 0.73 | 0.25 | — |
| 90–99 | 0.87 | 0.25 | 3000 |
| 100–109 | 1.06 | 0.25 | 2000 |
| 110–119 | 1.37 | 0.25 | 1000 |

$\lambda = 0.95$, $M = 0.05$

change in the size compositions predicted by the model.

It might be assumed that the model is unrealistic in considering only four size classes with a range of 80–119 mm carapace length, and simulations involving more size classes tend to reduce the effect of the density-dependent process. It is, however, self-evident that catch-at-length data which have large numbers of individuals in the large size classes are unlikely to have tight limits on the numbers that can enter such size classes. In fact, for areas such as north Norfolk where the substrate is not suitable for large lobsters, almost the entire catch is within the range 80–119 mm carapace length (Bannister et al. 1983). Indeed, estimates of fishing mortality from size compositions are determined in most fisheries for this size range only, as catch-at-length data for larger size classes with very few individuals can be inaccurate due to sampling errors.

If an overcompensatory stock–recruitment curve (e.g. $\beta = 2.0$) is used in the model, i.e. "scramble" competition (Nicholson 1954), so that the recruitment curve is equivalent to that of Ricker (1954), then the dampening effect of changes in size composition due to changes in fishing effort may be particularly marked. At low levels of fishing mortality, and hence high densities of individuals (on the descending loop of the curve), recruitment to a particular size class may be considerably reduced. Conversely, a drop in population density caused by increased fishing effort will actually increase recruitment to the larger size classes.

Clearly, the influence of the density-dependent recruitment depends on the strength of that density dependence or the maximum number of large individuals that the substrate can support in comparison with the number of recruits. If the model incorporates variable recruitment as well as density-dependent natural mortality, then the model may predict unexpected changes in size compositions when the pattern of exploitation changes. For example, if the model is used to simulate the fate of 10 000 recruits to the fishery based on the parameters of Table 3, then the size composition of Fig. 6a is generated. Consider, then, a doubling in fishing effort with a concurrent reduction of 50% in recruitment to 5000 recruits to the 80 mm size class. The model then generates the size composition shown in Fig. 6b, which would suggest that fishing mortality had in fact *decreased*.

## Discussion

Some assumptions concerning the biology and behaviour of lobsters remain to be discussed. The problem of ageing lobsters means that this model is based on length compositions and therefore is subject to the many shortcomings of using length-based data.[1] Secondly, there are aspects of moulting behaviour which suggest that this model may be inaccurate. The model would seem to assume that the lobster moults and if it cannot find a suitable shelter it will be swept away and will die. Similarly, the model assumes that lobsters will always moult after a specified period of time. In fact, studies of lobster behaviour suggest that the lobster finds a shelter and then moults; it may delay moult if it cannot find a shelter (B. T. Hepper, MAFF, Conwy, England, pers. comm.). Finally, Thomas (1958) suggested that small lobsters normally moult before large ones. As the large lobsters would be occupying the large holes, they would exclude any smaller individuals that had moulted already. Under these circumstances the small individuals may also delay moult.

A more realistic model would assume therefore that lobsters which do not find a suitably larger shelter will delay moult, and thus the function $S$ in equation 3 should depend on the numbers which reach time $t + \Delta t$ plus individuals in the next size class which have not moulted. However, these observations on moulting behaviour would serve to enhance the effect of the substrate limitation factor. At reduced densities a higher proportion would moult whereas at low levels of exploitation and

[1]FAO/ICLARM/KISR Conference on Theory and Applications of Length-Based Methods of Stock Assessment (Sicily, February 1985).

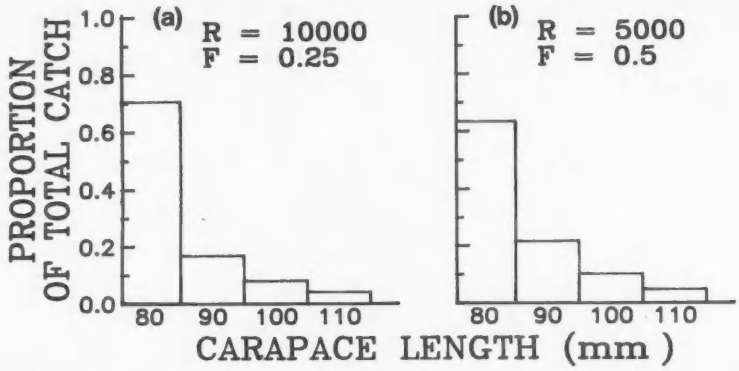


FIG. 6. Predicted size composition of catch for model B when (a) $R = 10\,000$, $F = 0.25$ and (b) $R = 5000$, $F = 0.5$.

high densities, many individuals would delay moult and hence give the impression that fishing mortality was still high.

This study has been restricted to one process that may underly the lack of correlation between fishing effort and fishing mortality. There may, however, be problems in the collation and interpretation of effort and size composition data. Technological advances ensure that indices of fishing effort are difficult to establish (e.g. Robinson 1979), and in trap fisheries, saturation of the grounds with traps may mean that changes in fishing mortality may not necessarily be proportional to observed changes in fishing effort (Conan 1984). Changes in size composition may be difficult to detect, particularly when recruitment fluctuates from year to year. Ricker (1963) suggested that changes in age (or size) composition in response to changes in exploitation are more marked in virgin fisheries than in established fisheries. Nevertheless, there are circumstances in which we might expect little change in size composition with time. Firstly, fishermen may fish subareas of a fishery in a cyclical manner dependent on local abundance of large lobsters (e.g. see Pezzack and Duggan 1983), with the resulting aggregation of size compositions from these subareas remaining constant. In this case, any increase in fishing effort would be due to a steady expansion of fishing grounds. Secondly, in the Norfolk fishery, for example, most of the catch is from the year class just recruited to the fishery (Bannister et al. 1983), and so size composition may simply reflect the variation in growth rate between individuals in the population. Thus abundance will change, but not size composition. Thirdly, a combination of declining recruitment and increasing fishing effort could produce a fairly stable size composition, but in this case there would be a concurrent decline in catch-per-unit-effort.

The results of this model may lead to a reexamination of the size compositions in many fisheries. For example, the high level of fishing mortality observed for lobsters in Norfolk (Bannister and Addison 1984) may be an overestimate by the Jones' length cohort analysis produced by apportioning too high a proportion of total mortality ($Z$) to the fishing mortality ($F$). This suggests that size-dependent natural mortality should be incorporated into the standard length cohort analysis model to obtain more realistic estimates of $F$, but it should be stressed that there are considerable problems involved in the estimation of mortality rates in natural populations (e.g. Campbell 1980). Nevertheless, it is essential that levels of fishing mortality should also be estimated from tagging experiments.

The relative importance of the density-dependent recruitment process and of the level of fishing mortality depends on the present density of individuals in a size class and the upper limit of numbers that the substrate can support. Clearly, if the population density is very low in comparison with the upper limit, then the relationship between actual recruitment and potential recruitment is almost linear, and the level of fishing mortality is the major determinant of the size composition of the population and catch. Conversely, if the population density of each size class is close to the natural limit, then changes in fishing mortality will have little effect on the size compositions, and density-dependent constraints will be limiting.

Despite the rather loose assumption of using 10-mm size classes as equivalent to a moult increment, and the inaccuracies of the Jones' length cohort technique, this model has shown that, by the addition of a density-dependent process to the standard yield per recruit model, changes in exploitation pattern may not necessarily be detected by observing the size composition. Coupled with some nonlinear relationship between increase in physical effort (i.e. boats × pots) and increase in effective effort on the ground, then large increases in fishing effort may actually cause the size composition of the catch to change very little. Similarly, with variable recruitment, analysis of size composition data may produce a completely false picture of the state of the fishery.

In view of the above problems and because possible delay of moulting at high densities makes the von Bertalanffy growth function inadequate even as a rough approximation to crustacean growth, it would be wise to reexamine current techniques for stock assessment of crustacean populations.

## Conclusions

The results generated by this model have three major implications for the management of crustacean fisheries.

(1) When catch and effort data are not available or unreliable, reliance on size composition data may mean that a serious decline of the fishery is not detected.

(2) Use of conventional cohort analysis for size composition data to estimate benefits to catch and stock biomass following a change in the pattern of exploitation may suggest contradictory advice to that based on the assumption that density-dependent mortality occurs among large lobsters.

(3) It is essential that the maximum densities of large lobsters that a substrate can support be quantified, and perhaps densities of lobsters on the ground should be measured in conjunction with size composition data. Estimates of the proportion of individuals that moult in each size class during the moulting season may provide an indication of the number of available shelters.

## Acknowledgements

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## References

ANONYMOUS 1979. Report of the *Homarus* Working Group. ICES C.M. 1979/K:8. (Mimeo.)

BANNISTER, R. C. A., AND J. T. ADDISON. 1984. The effect on yield and biomass per recruit of changes in fishing mortality and size at first capture in the fisheries for lobster, *Homarus gammarus* L., in England and Wales. ICES C.M. 1984/K:10. (Mimeo.)

BANNISTER, R. C. A., J. T. ADDISON, S. R. J. LOVEWELL, AND A. E. HOWARD. 1983. Results of a recent minimum size assessment for the fisheries for lobster, *Homarus gammarus*, in England and Wales. ICES CM 1983/K:4. (Mimeo.)

CAMPBELL, A. 1980. A review of mortality estimates of lobster populations in the Canadian maritimes. Can. Tech. Rep. Fish. Aquat. Sci. 932: 27–36.

1985. Application of a yield and egg-per-recruit model of the lobster fishery in the Bay of Fundy. N. Am. J. Fish. Manage. 5: 91–104.

CONAN, G. Y. 1984. Do assumptions commonly used for modelling populations of finfish apply to shellfish species? ICES C.M. 1984/K:49. (Mimeo.)

ENNIS, G. P. 1980. Canadian efforts to assess yield per recruit in lobsters. Can. Tech. Rep. Fish. Aquat. Sci. 932: 45–48.

FOGARTY, M. J. 1980. Assessment of yield-per-recruit for the American lobster (*Homarus americanus*). Can., Tech. Rep. Fish. Aquat. Sci. 932: 37–44.

FOGARTY, M. J., R. A. COOPER, J. R. UZMANN, AND T. BURNS. 1982. Assessment of the offshore American lobster (*Homarus americanus*) fishery. ICES C.M. 1982/K:14. (Mimeo.)

HEPPER, B. T. 1967. On the growth at moulting of lobsters (*Homarus vulgaris*) in Cornwall and Yorkshire. J. Mar. Biol. Assoc. U.K. 47: 629–643.

1978. Population dynamics of the lobster *Homarus gammarus* (L.) off the coasts of England. Fish. Res. Tech. Rep. MAFF Direct. Fish. Res. Lowestoft 41: 29 p.

HOWARD, A. E. 1980. Substrate controls on the size composition of lobster (*Homarus gammarus* L.) populations. J. Cons. Int. Explor. Mer 39: 130–133.

HOWARD, A. E., AND R. S. NUNNY. 1983. Effects of near-bed current speeds on the distribution and behaviour of the lobster, *Homarus gammarus* (L.). J. Exp. Mar. Biol. Ecol. 71: 27–42.

JONES, R. 1974. Assessing the long term effects of changes in fishing effort and mesh size from length composition data. ICES C.M. 1974/F:33. (Mimeo.)

1981. The use of length composition data in fish stock assessments (with notes on VPA and cohort analysis). FAO Fish. Circ. 734: 55 p.

NICHOLSON, A. J. 1954. An outline of the dynamics of animal populations. Aust. J. Zool. 2: 9–65.

PEZZACK, D. S., AND D. R. DUGGAN. 1983. The Canadian offshore lobster (*Homarus americanus*) fishery — 1971 to 1982. ICES C.M. 1983/K:34. (Mimeo.)

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

1963. Big effects from small causes: two examples from fish population dynamics. J. Fish. Res. Board Can. 20: 257–264.

ROBINSON, D. G. 1979. Consideration of the lobster (*Homarus americanus*) recruitment overfishing hypothesis; with special reference to Canso Causeway. Fish. Mar. Serv. Tech.Rep. 834: 77–99.

SHEPHERD, J. G. 1982. A versatile new stock–recruitment relationship for fisheries, and the construction of sustainable yield curves. J. Cons. Int. Explor. Mer 40: 67–75.

SKUD, B. E. 1969. The effect of fishing on size composition and sex ratio of offshore lobster stocks. Fiskeridir Skr. Ser. Havunders. 15: 295–309.

THOMAS, H. J. 1958. Some seasonal variations in the catch and stock composition of the lobster. J. Cons. Int. Explor. Mer 24: 147–154.

TVEITE, S., AND C. J. RØRVIK. 1982. A stock assessment of lobster (*Homarus gammarus*) on the Norwegian Skagerrak coast. ICES C.M. 1982/K:7. (Mimeo.)

# Recruitment Dynamics in an American Lobster (*Homarus americanus*) Population

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Fogarty, M. J., and J. S. Idoine. 1986. Recruitment dynamics in an American lobster (*Homarus americanus*) population. Can. J. Fish. Aquat. Sci. 43: 2368–2376.

We examined relationships between successive life history stages of an American lobster (*Homarus americanus*) population for evidence of density-dependent control. Analysis of a time series of larval production estimates for the Northumberland Strait region of the southern Gulf of St. Lawrence during 1949–63 (D. J. Scarratt. 1964. J. Fish. Res. Board Can. 21: 661–680; D. J. Scarratt. 1973. J. Fish. Res. Board Can. 30: 1819–1824) provided no indication of density-dependent regulation during the pelagic larval phase. However, an asymptotic relationship between the final (fourth) larval stage and stock size 5–7 yr later was demonstrated, indicating the possibility of density-dependent regulation between larval settlement and subsequent recruitment to the fishery. A second analysis supported these results based on trends in population size over several generations. A recruitment mechanism of this type is highly stabilizing and can explain the apparent capacity of lobster populations to sustain high levels of fishing mortality. The postulated recruitment mechanism for Northumberland Strait lobsters may reflect competition for critical resources. We propose that shelter is an important limiting resource and that shelter competition experiments be undertaken in the field and laboratory to test this hypothesis. Finally, we demonstrate the use of a multistage recruitment model which accounts for the general form of observed interstage relationships. The asymptotic relationship between stage IV production and subsequent stock results in a stable population which is resilient to exploitation.

Nous avons examiné les relations entre les divers stades successifs de développement d'une population de homards (*Homarus americanus*) pour relever des signes d'une régulation dépendante de la densité. L'analyse d'une série chronologique d'estimations sur la production de larves dans la région du détroit de Northumberland, dans le sud du golfe du Sainte-Laurent, entre 1949 et 1963 (D. J. Scarratt. 1964. J. Fish. Res. Board Can. 21: 661–680; D. J. Scarratt. 1973. J. Fish. Res. Board Can. 30: 1819–1824) n'a donné aucune indication d'une régulation de ce type pendant la phase larvaire pélagique. Toutefois, il apparaît une relation asymptotique entre le dernier (quatrième) stade larvaire et la taille du stock 5 à 7 ans plus tard, ce qui indique qu'il peut se produire une régulation dépendante de la densité entre l'établissement des larves sur le fond et le recrutement subséquent pour la pêche. Ces résultats sont étayés par une deuxième analyse fondée sur les tendances de la taille de la population sur plusieurs générations. Une mécanisme de recrutement de ce type a un fort effet stabilisateur et peut expliquer l'aptitude apparente des populations de homards à supporter un taux élevé de mortalité par pêche. Le mécanisme de recrutement dont nous postulons l'existence chez les homards du détroit de Northumberland peut signaler une compétition autour de ressources critiques. Nous posons que l'abri peut constituer une importante ressource limitante, et nous proposons d'effectuer des expériences sur la concurrence dans la recherche d'abri, sur le terrain et en laboratoire, afin de vérifier cette hypothèse. Enfin, nous démontrons l'emploi d'un modèle du recrutement multistade qui tient compte de la forme générale des relations observées entre les stades. La relation asymptotique entre la production du stade IV et le stock subséquent produit une population stable qui réagit bien à l'exploitation.

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The life cycle of the American lobster, *Homarus americanus*, is complex (sensu Wilbur 1980). Several life history stages occur, each with different ecological characteristics. Density-dependent regulation may be important at one or more points in the life cycle. An understanding of the nature of population control is crucial in evaluating the resilience of lobster populations to exploitation. The American lobster supports an extremely valuable commercial fishery and exploitation rates are typically high. The level of fishing pressure that lobster populations can sustain without adverse effects on recruitment, however, is currently unknown.

Hancock (1973) observed that the form of population regulation is known for few crustacean species. However, recent studies of the western Australian rock lobster, *Panulirus cygnus* (Morgan et al. 1982), blue crab, *Callinectes sapidus* (Tang 1985), king crab, *Paralithodes camtschatica* (Reeves 1982), Dungeness crab, *Cancer magister* (Botsford and Wickham 1975, 1978; Botsford 1984; McKelvey et al. 1980), and the prawns *Penaeus esculentus* and *P. merguiensis* (Penn and Caputi 1985; Staples 1985) have considerably advanced our understanding of recruitment processes in crustacean populations. Environmental factors and spawning stock levels were shown to have important effects on recruitment in several of these species.

Stock–recruitment relationships are often highly variable (Sissenwine 1984). Recruitment variability can be attributed to variation in biotic and abiotic environmental factors. Density-independent effects are unquestionably important; however, the form of population regulation (if any) must be understood to determine the probable response to exploitation. Populations with little or no capacity for compensatory population regulation will be particularly vulnerable to overexploitation. It is therefore important to determine whether the population exhibits some form of compensation.

In this paper, we attempt to identify recruitment mechanisms in an American lobster population. Long-term studies of larval lobster production and exploitable stock size for Northumberland Strait in the southern Gulf of St. Lawrence (Scarratt 1964, 1973) are reevaluated for evidence of density-dependent population control. American lobster populations are subjected to annual fishing mortality rates of 85–90% (Anthony 1980; Campbell 1980), yet relatively few instances of stock collapse have been recorded. Our objective is to determine whether stabilizing forms of population regulation can be identified for lobster stocks. We then consider the resilience of a lobster population to exploitation under alternative recruitment mechanisms.

## Methods

### Data Sources

Larval lobster surveys were conducted in Northumberland Strait of the southern Gulf of St. Lawrence during 1948–63 (Wilder 1953; Scarratt 1964, 1973). Data for 1948 were preliminary and were not further considered. Neuston tows were made at 23 sites during 1949–61; this number was reduced to 15 during 1962–63 and the arrangement of stations was altered. Estimated surface area sampled during a tow averaged 3430 $m^2$ based on vessel speed, tow duration, and net width. Scarratt (1964) provided a detailed description of sampling design and methodology. Scarratt adjusted density estimates of each larval stage for developmental time at prevailing water temperatures and standardized these results to estimate weekly larval production. These estimates were integrated to calculate production over the season.

Paloheimo (1963) made population estimates for the exploitable stock for the Miminigash region of Northumberland Strait during 1946–58 based on mark–recapture experiments. Scarratt (1964, 1973) extended these results to 1969 and examined predictive relationships between stage IV production and subsequent stock size. Adjustments to the stock size estimates were necessary to account for variability in growth rates. A cohort may recruit to the fishery over 5–7 yr in Northumberland Strait (Wilder 1953). Scarratt (1973) took 3-yr running averages of both stage IV production and resulting stock size to adjust for this partial recruitment pattern. Fogarty (1983) followed this same procedure. In the present analysis, we employed a weighted average of stock size with weights of 0.25, 0.50, and 0.25 for ages 5, 6, and 7, respectively. Weighting factors were based on growth of laboratory-reared lobsters (Hughes and Matthiessen 1962) which demonstrated a symmetrical distribution of age-at-length. We also examined the implications of different periods of averaging (4–6 and 6–8 yr); varying the period of averaging did not change the general form of the relationship nor did the use of an unweighted average. In the absence of a clear biological rationale, stage IV production estimates were not averaged. It was recognized, however, that also averaging the larval production estimates (Scarratt 1973; Fogarty 1983) has the effect of smoothing random variation in the estimates.

Estimates of the exploitable stock (Paloheimo 1963; Scarratt 1964, 1973) were not limited to recruits. Exploitation rates during 1946–58 at Miminigash averaged 0.72 (calculated from Paloheimo 1963). It is reasonable to assume that under these relatively high exploitation rates, recruits were a dominant component of the exploitable stock. Accordingly, we have used the stock estimates as an index of recruitment (see also Scarratt 1964, 1973).

### Analysis

Descriptive characteristics of larval production and stock size estimates were first examined. We used a simple turning point test (e.g. Seigel 1956, p. 55.; Sokal and Rohlf 1981, p. 782–787) to test for randomness in each of the time series. Trends in the series would result in a significant number of "runs" or sequences of similar estimates. We also examined trends in mortality rates between successive larval stages. Mortality rates were calculated as $\ln (P_i/P_{i+1})$ where $P_i$ is the seasonal production of the $i$th larval stage.

We used several approaches to evaluate density dependence. First, relationships between successive life history stages were examined. We assumed that density-independent relationships would be characterized by linear functions through the origin and that nonlinear relationships would reflect density- or stock-dependent (Harris 1975) relationships. A linear funtion through the origin (i.e. a density-independent model) was considered the appropriate null model. Any model with a nonzero intercept cannot be appropriate for a closed population. The classical Beverton–Holt (1957) and Ricker (1954) stock–recruitment models were used as functional forms for asymptotic and dome-shaped relationships, respectively.

Bulmer (1975) and Slade (1977) suggested tests for density dependence using population census data. In the absence of density dependence, the appropriate population model may be expressed (see Appendix):

$$\ln N_{t+r} = a' + b' \ln N_t$$

where $N_t$ is the population size at time $t$, $r$ is a time delay, $a'$ is a model parameter, and $b' = 1.0$ (the primes distinguish these parameters from symbols used later). For the density-dependent case, $b' < 1.0$. Slade (1977) noted that measurement error in both variables invalidated the use of ordinary least squares regression and suggested instead the use of the principal axis of the bivariate relationship (see Ricker 1973 and Jolicoeur 1975 for related discussions). Bulmer (1975) derived an estimator of the slope based on the first-order autocorrelation coefficient in recognition of the time series nature of the population estimates. Bulmer (1975) also provided an alternative estimator which was less sensitive to measurement error. We applied these tests to the Northumberland Strait population estimates made by Paloheimo (1963) and Scarratt (1964, 1973).

## Results

### Larval Production

Larval production fluctuated about relatively fixed levels during 1949–63 (Fig. 1). No significant trends were evident

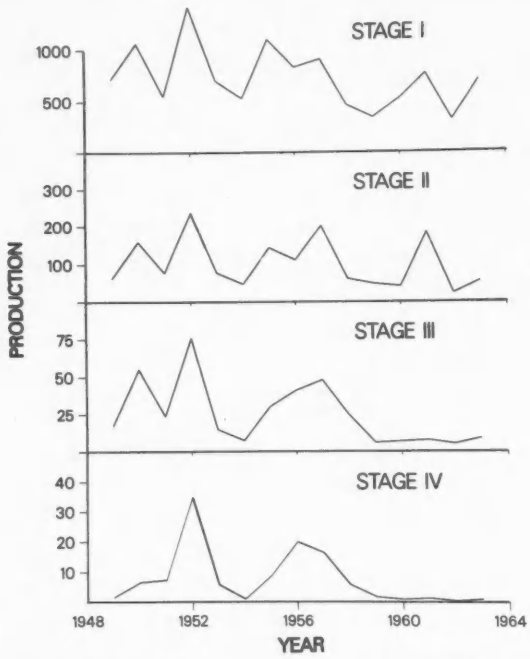


FIG. 1. Trends in annual larval production (no. per 3430 $m^2$ adjusted for development time) for each of the larval stages in western Northumberland Strait during 1949–63.

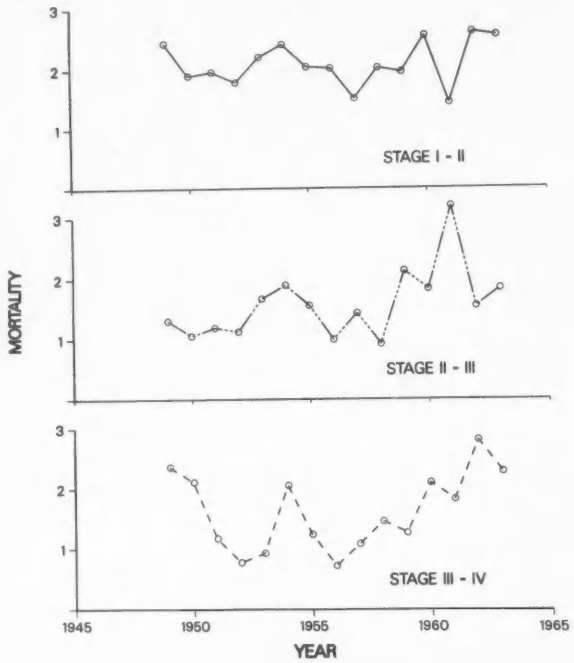


FIG. 2. Trends in instantaneous mortality between successive larval stages in western Northumberland Strait during 1949–63. Mortality estimated by the relationship $M = \ln(P_i/P_{i+1})$ where $P_i$ is the annual production of the $i$th larval stage.

TABLE 1. Summary statistics for annual larval production estimates (no. per 3430 $m^2$) (Scarratt 1964, 1973) in the Northumberland Strait region during 1949–63. C.V. = coefficient of variation; Z = test statistic for a simple turning point test (Seigel 1956); * significant at $p < 0.05$ (significance level is provided in parentheses).

| | Stage I | Stage II | Stage III | Stage IV |
|---|---|---|---|---|
| Mean | 722.35 | 101.78 | 24.69 | 7.47 |
| SE | 76.88 | 17.88 | 5.45 | 2.46 |
| C.V. | 41.22 | 64.71 | 86.99 | 127.65 |
| Z | 0.00 | −0.521 | −2.136* | −1.597 |
| | (1.00) | (0.603) | (0.033) | (0.110) |

for stages I, II, and IV based on a turning point test ($p > 0.05$). However, we detected a significant decreasing trend for stage III (Table 1). Scarratt (1973) noted a tendency for reduced larval production during the latter years of the survey; estimates during 1962–63 were the lowest in the series for stages II–IV. Interannual variability in larval production increased from stage I to stage IV. Coefficients of variation increased from 41% at stage I to over 100% at stage IV. Larval mortality rates were also variable and appeared to increase over time (Fig. 2); however, we found no significant ($p > 0.05$) trends in mortality (Table 2). Mean survival between stages I and II, II and III, and III and IV was 12.5, 20.6, and 20.0%, respectively. Survival from stage I through the approximate midpoint of the fourth stage averaged 0.86% during 1949–63.

We found no indication of density dependence during the pelagic larval stages. Interstage relationships were linear with no indication of compensation at high larval densities (Fig. 3; Table 3). In contrast, the relationship between stage IV production and the weighted average of subsequent stock size was asymptotic (Fig. 4), indicating the possibility of density-dependent control during the period between settlement of the fourth larval stage and recruitment to the fishery 5–7 yr later. We fit the Beverton–Holt model to these data by nonlinear least squares in the form $R = S/(aS + b)$ where $R$ is the recruitment index (averaged stock size), $S$ is stage IV production, and $a$ and $b$ are parameters. Estimates for the coefficients were $a = 0.000257$ (SE = 0.0000209) and $b = 0.00006231$ (SE = 0.0000379). Standard tests of significance do not apply for nonlinear estimation. It is clear, however, that the density-dependent parameter ($a$) is characterized by a low standard error and is statistically significant (exact probability level cannot be specified). The density-independent parameter ($b$) had a relatively large standard error and was not reliably determined. The model provides a useful representation of the functional form of the stage IV − stock size relationship. Variability in the relationship, however, limits its utility in forecasting recruitment to the fishery.

Frequency distributions of larval production were asymmetrical for each stage (Fig. 5). Production was increasingly skewed toward lower levels at successive larval stages. The frequency distribution of mortality rates between stages I and II was symmetrical (Fig. 6) but less so for later stages.

## Exploitable Stock

Estimated stock size for the Miminigash region varied around a mean level of 330 000 lobsters during 1949–69 (Fig. 7); the coefficient of variation was 30%. We obtained no evidence of density dependence at a lag of 1 yr (i.e. abundance

TABLE 2. Summary statistics for instantaneous mortality rates ($\ln(P_i/P_{i+1})$) between successive larval stages (Scarratt 1964, 1973) in the Northumberland Strait region during 1949–63. $P_i$ = seasonal production estimate for stage $i$; C.V. = coefficient of variation; $Z$ = test statistic for a simple turning point test (Seigel 1956); significance level is provided in parentheses.

| | Stages I–II | Stages II–III | Stages III–IV |
|---|---|---|---|
| Mean | 2.080 | 1.581 | 1.618 |
| SE | 0.093 | 0.149 | 0.168 |
| C.V. | 17.352 | 36.497 | 40.190 |
| $Z$ | −0.168 | −0.194 | −0.521 |
| | (0.866) | (0.052) | (0.603) |

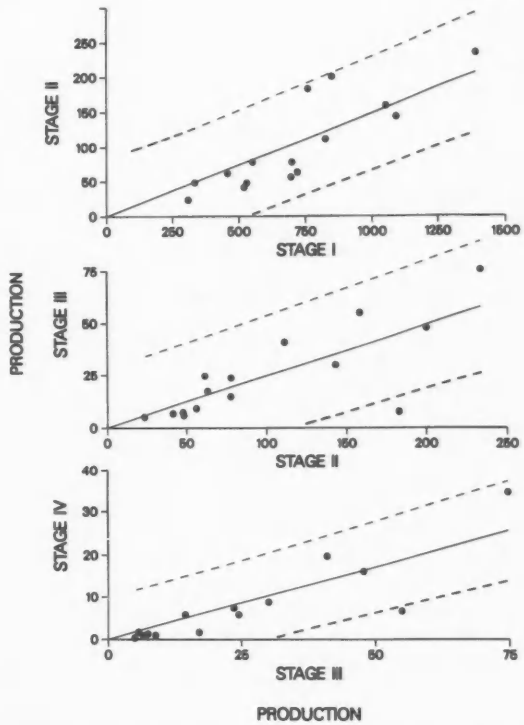


FIG. 3. Relationships between successive larval stages in western Northumberland Strait during 1949–63. Lines forced through the origin. Points represent observed values. Broken lines indicate 95% confidence intervals.

levels in one year did not affect those in the following year; Table 4). The slope of the relationship between stock size in adjacent years did not differ significantly from 1.0 by the methods of Bulmer (1975) and Slade (1977). In contrast, tests for density dependence at lags of 6 and 7 yr (approximately one generation) provided evidence for delayed regulation; the slopes differed significantly from 1.0.The slope for a lag of 5 yr was characterized by a large standard error and the approximate confidence intervals included 1.0 (i.e. the density-independent model could not be rejected). Results for lags of 6–7 yr, however, are consistent with inferences drawn earlier and support the hypothesis of density-dependent control during the early life history stages.

TABLE 3. Parameters and associated statistics for linear models relating successive larval stages. Lines were forced through the origin. Standard errors are provided in parentheses; $D$ = Durbin–Watson statistic for first-order autocorrelation in residuals; * significant at $p < 0.05$. Significant test statistic indicates that residuals are not independently distributed and therefore assumptions of model are not met; this does not affect the interpretation used here.

| | Stages I–II | Stages II–III | Stages III–IV |
|---|---|---|---|
| Slope | 0.148 | 0.247 | 0.340 |
| | (0.012) | (0.028) | (0.037) |
| $r^2$ | 0.92 | 0.84 | 0.86 |
| $D$ | 2.167 | 1.856 | 1.527* |

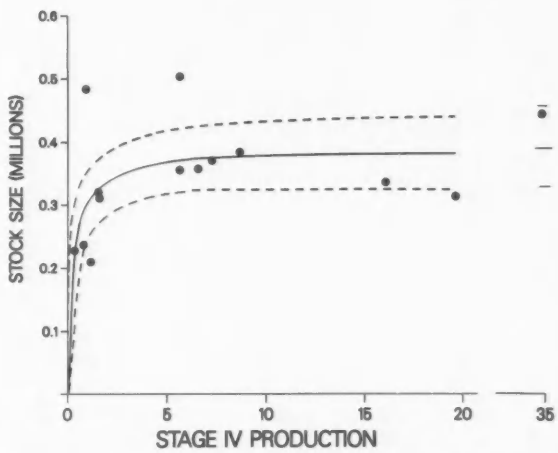


FIG. 4. Relationship between stage IV production (no. per 3430 $m^2$ adjusted for development time) and weighted average for a subsequent stock size. Points represent observed values. Beverton–Holt model fitted to data (solid line). Broken lines represent ±2 SE.

## Multistage Model

Information on the form of interstage relationships may be synthesized in a multistage recruitment model (see Paulik 1973). We will deal with a simplified representation of this system. For the model, we require information on the following relationships: (1) spawning stock size and stage I production, (2) stage I production and stage IV production, (3) stage IV production and recruitment to the fishery, and (4) recruitment and spawning stock size. These relationships define one complete cycle of the life history.

Direct estimates of spawning stock size were not available. We assumed a linear relationship between spawning stock and stage I production, since density dependence in either egg or stage I production has not been conclusively demonstrated (however, see Discussion). Relationships between successive larval stages are linear (Fig. 3). Therefore, the relationship between stage I and stage IV production may be represented by a linear function. Empirical evidence indicated an asymptotic relationship between stage IV production and recruitment (Fig. 4). Finally, a linear relationship was used to model the relationship between recruitment and spawning stock size, since survival from recruitment (to the fishery) to reproductive age is assumed to be directly proportional to the total mortality rate. Note that the position of this line will change as fishing

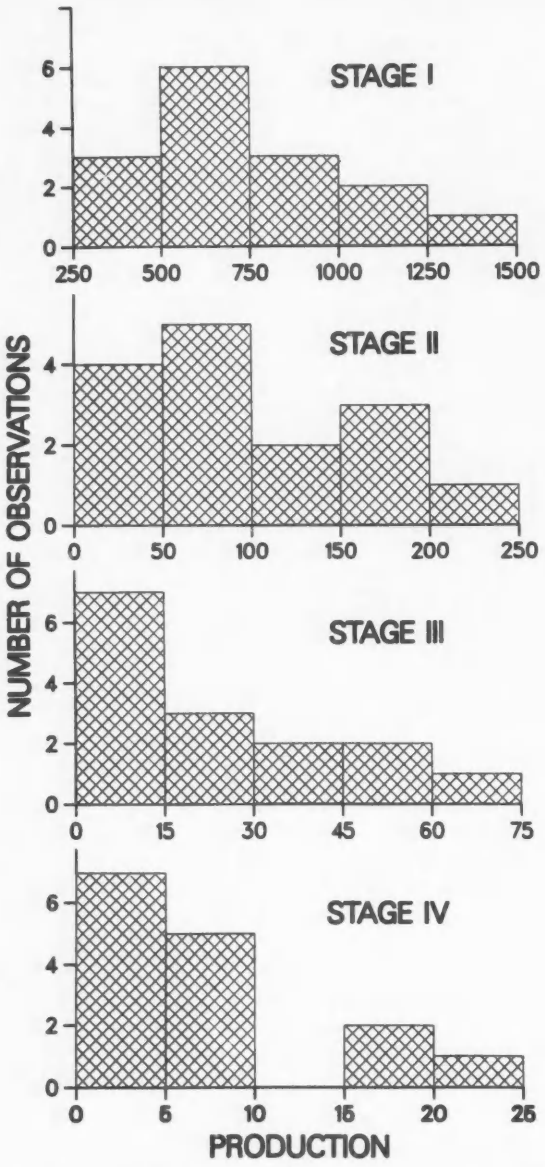


FIG. 5. Frequency distributions of production (no. per 3430 $m^2$ adjusted for development time) for each larval stage in western Northumberland Strait during 1949–63.

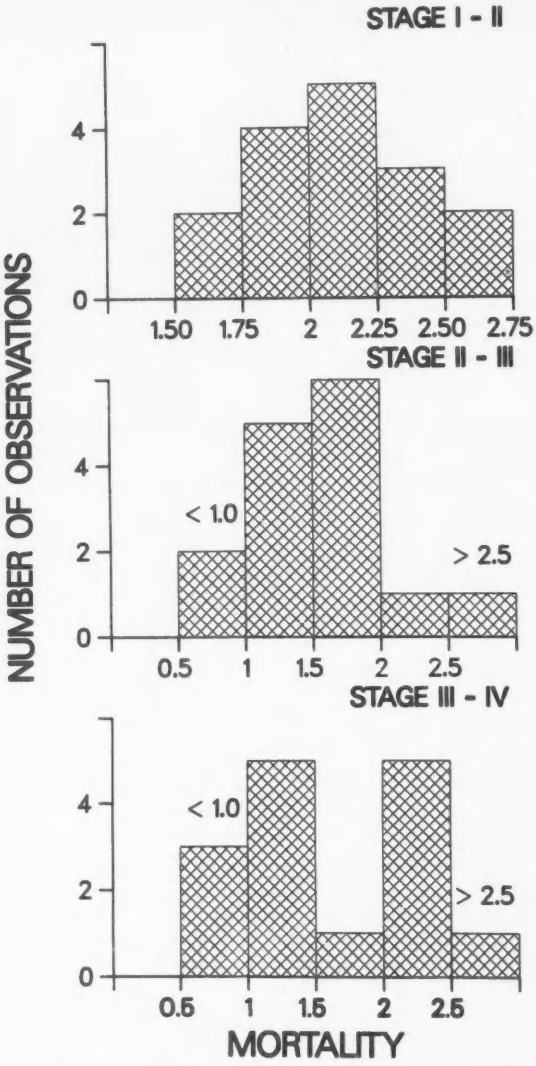


FIG. 6. Frequency distributions of mortality between successive larval stages in western Northumberland Strait during 1949–63. Mortality estimated by the relationship $M = \ln (P_i/P_{i+1})$ where $P_i$ is the production of the $i$th larval stage.

mortality rates vary. The general forms of these relationships are illustrated in Fig. 8; the depicted forms do not represent actual fitted relationships. The figure is divided into four quadrants, each representing one of the interstage relationships. To determine projected changes in population levels from some initial spawning stock size, follow the sequence of letters starting at position A. Note that after one generation (position I), the parental stock has increased. However, after a second generation (position Q), the parent stock has changed little from the previous level. This is due to the stabilizing effect of the asymptotic relationship between stage IV production and recruitment (quadrant 3). It is easy to see that if the relationships in each quadrant were linear (i.e. no density dependence in the life cycle), the population would either continually increase or decrease except under restricted conditions. Note also that as fishing mortality increases, reduced population levels would result. This may be seen by tracing the population trajectory resulting if the line labelled F2 in quadrant 4 is used as the transfer line. The main point is that the apparent form of population regulation between settlement and recruitment to the fishery is stabilizing. This is consistent with empirical observation. It is also clear that increased levels of fishing mortality

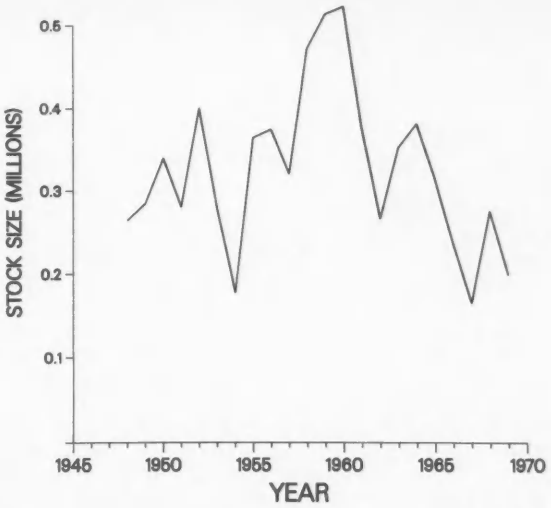


FIG. 7. Trends in estimated stock size for the Miminigash region of western Northumberland Strait during 1949–69 determined by mark–recapture experiments.

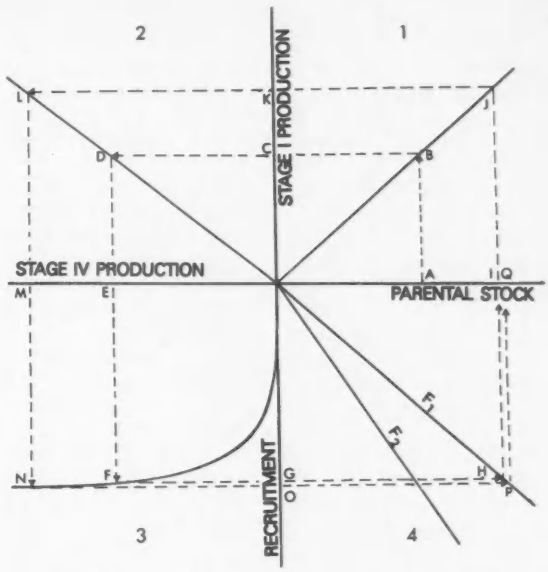


FIG. 8. Relationships between successive life history stages of the American lobster in western Northumberland Strait. Quadrants 1–4 illustrate the general forms of the relationships between parent stock and stage I, stages I and IV, stage IV and recruitment, and recruitment and parent stock. One complete generation is defined. See text for further explanation.

may result in sharply reduced population size. If the slope of the curve relating stage IV production and recruitment is steep at the origin, high levels of fishing mortality might be sustained with little or no warning of an impending stock collapse until critical mortality levels are reached.

## Discussion

How do lobster populations persist under extremely high levels of fishing? We reexamined a time series of larval production and stock size estimates for evidence of stabilizing forms of population regulation. Density-dependent control was indicated by two lines of evidence: (1) an asymptotic relationship between stage IV production and subsequent stock size and (2) results of a test for density dependence based on trends in population size. The first demonstrated that stock size was relatively constant over a broad range of stage IV larval production. Extremes of stage IV production did not markedly affect resulting stock size, although an indication of reduced stock size with low larval production was obtained. The observed asymptotic recruitment relationship is consistent with competition for limiting resources. Shelter availability is a critical feature of lobster habitat (Cobb 1971) and competition for shelter sites may play a central role in lobster population dynamics. Postsettlement lobsters in particular are vulnerable to a broad range of predators. Locating and successfully occupying and defending a shelter site is critical for survival. Stage IV lobsters preferentially settle in substrates where shelter is available (Cobb 1968; Botero and Atema 1982). The larval dispersal phase reduces competition. Despite high mortality rates in the plankton, mortality would presumably be higher without dispersal or selection pressure would favor elimination of the planktonic phase. The importance of shelter competition may be tested by resource addition or removal experiments.

Interannual variability in larval lobster production increased with successive larval stages. Distributions of larval production were skewed toward lower levels, while distributions of mortality rates were more symmetrical. These observations agree with patterns in recruitment and mortality for a number of marine organisms (see Peterman 1981; Hennemuth et al. 1980; Beddington and Cooke 1983; Garrod 1982, 1983). Clearly, the use of a deterministic recruitment model is simplistic. Our observations are consistent with an underlying density-dependent recruitment model subject to random variation in mortality rates. Interestingly, observations on recruitment patterns in other marine invertebrates (e.g. Loosanoff 1964, 1966; Caffey 1985) indicate much higher levels of variability, spanning several orders of magnitude in some cases. Lobsters are characterized by relatively low fecundity, large egg size (high

TABLE 4. Test statistics for density independence in lobster populations in western Northumberland Strait. The estimator ($b'$) is the slope of the principle axis of the relationship between population size at time $t$ and at various lags (Slade 1977). Approximate upper (U95) and lower (L95) 95% confidence intervals of the slope are provided. The test statistics $R$ and $R^*$ were proposed by Bulmer (1975) as tests for density independence. **95% confidence intervals on slope of principal axis overlap 1.0; hypothesis of density independence is accepted at the 0.05 level. †Not significant at the 0.05 level; hypothesis of density independence is accepted.

| | 1 | 5 | 6 | 7 |
|---|---|---|---|---|
| $b'$ | 0.877** | −0.106** | −0.662 | −0.689′ |
| U95 | 0.251 | 1.924 | −0.001 | −0.006 |
| L95 | 2.538 | −3.663 | −2.288 | −2.197 |
| $R$ | 0.926† | | | |
| $R^*$ | −0.196† | | | |

energetic investment), and additional parental investment (brooding the ova). For a review, see Hazlett (1983). The protection of the eggs through the 9- to 12-mo incubation period undoubtedly reduces variability in survival rates. Crustacean species with lower parental investment (e.g. penaeid shrimp) appear to have more variable, environmentally driven recruitment patterns.

Scarratt (1973) concluded that it was not possible to accurately predict stock size from stage IV production. We were primarily interested in the form of recruitment function and not in prediction per se. Relationships between successive life history stages were sufficiently well defined to discern their general form. Clearly, there are numerous biotic and abiotic factors which affect recruitment and it is unlikely that any single factor would explain most of the variation in recruitment. Consideration of environmental factors in addition to spawning stock improved the predictive capability of recruitment models for a number of crustacean species (e.g. Tang 1985; Penn and Caputi 1985; Staples 1985). We did not attempt to incorporate environmental variables in the model but note that Sutcliffe (1973) reported a significant relationship between river discharge and larval lobster production in Northumberland Strait. Sutcliffe postulated a linkage between runoff and primary production which affects larval survival. Caddy (1979) related larval lobster survival to a nonlinear temperature effect. Consideration of these environmental variables in the recruitment model could conceivably improve its forecasting capability.

Scarratt (1964) made a detailed analysis of within-season variation for the 1961 Northumberland Strait larval lobster survey. Significant spatial and temporal effects were noted. Scarratt provided variance estimates for annual production of stages I and IV during the 1961 season; coefficients of variation were 11 and 13%, respectively. The within-season variability was therefore considerably lower than the interannual variation in larval production (see Table 1). Year to year variation was highest for stage IV production. A potentially important source of variation in estimating production for this stage is variability in settlement times. Stage IV larvae settle to the bottom during the fourth larval stage (Scarratt 1973). J. S. Cobb (University of Rhode Island, Kingston, RI, pers. comm.) has suggested that there may be substantial variability in the timing of settlement. Since this factor directly affects the length of time that the fourth stage is vulnerable to neuston gear, estimates of stage IV production are subject to an additional source of measurement error. Coupled with the difficulty in sampling planktonic organisms with patchy distributions and the cumulative effects of random variation in mortality rates during the pelagic larval stages, it is not surprising that stage IV production estimates are more variable than earlier stages.

An important factor in any evaluation of lobster recruitment processes in Northumberland Strait is whether the larval production and stock size estimates are representative of the population in this region. Caddy (1979) analyzed changes in the center of distribution for successive larval stages and concluded that the larvae are probably maintained within the survey area. If larvae were known to be transported out of the western strait, use of these estimates would be compromised. Stock size estimates for Miminigash, P.E.I., cover only a portion of the area included in the larval lobster survey. To the extent that these estimates may not be representative of population trends in the survey region as a whole, an additional source of error would be introduced. Migration of juveniles and adults into or out of the region could also affect these relationships. Juvenile lobsters appear to be nonmigratory and may remain within burrow systems for extended periods (Cooper and Uzmann 1980). Movement of late juveniles and early adults is also generally restricted (e.g. Wilder 1963). We have therefore assumed that the larval production and stock estimates are useful indicators of population trends in the western Northumberland Strait.

No direct estimates were available to specify the relationship between spawning stock size and stage I production in the multistage model. Scarratt (1964, 1973) noted that with the exception of three years, trends in stage I production paralleled those in total stock size; for these three years, low stage I production occurred at high total stock size. If it is assumed that the spawning stock was at a high level during this period, a density-dependent effect on egg production or survival would be indicated (Scarratt 1964). Reduced fecundity at high densities could result from several factors such as reduced energy available for reproduction. An alternative mechanism might be an outbreak of *Pseudocarcinomertes homari*, a nemertean worm which attacks the egg mass of lobsters (see Campbell and Brattey 1986). Unfortunately, historical records of egg infestation by the nemertean are not available. Density-dependent transmission of the nemertean could result in a nonlinear relationship between spawning stock and stage I production. A highly nonlinear relationship of this type could induce population oscillations (although the asymptotic relationship between stage IV production and subsequent stock would tend to damp the oscillations). There was in fact some indication of cyclic trends in estimated stock size (Fig. 7); however, they were not statistically significant. It is possible that oscillations would be detectable with a longer time series of population estimates. Studies of density-related factors in the transmission of the nemertean would be desirable.

Observed patterns of recruitment in relation to larval production provide a possible explanation for the relative stability of the lobster stock in western Northumberland Strait and its apparent resilience to exploitation. Any conceptual model of lobster population dynamics must account for these characteristics. Empirical observations indicate that the population could conceivably sustain high levels of fishing mortality with little indication of decline; however, the stock would not be immune to recruitment overfishing. The level of fishing pressure that the population could withstand would depend on the slope of the relationship between recruitment and stage IV production at the origin. A steep slope would permit a relatively high level of exploitation before any indication of stock decline. The stock would decline precipitously, however, once a critical level of fishing mortality was reached. Robinson (1979) documented trends in commercial production, fishing effort, and population characteristics for lobster fisheries in the Maritime provinces and concluded that recorded stock collapses could in fact be attributed to recruitment overfishing.

An alternative explanation for the apparent resilience of lobster populations is that "refugia" exist in which some segment of the population is unexploited or less heavily exploited and this segment is capable of supplying recruitment for the entire population. The refugium may represent an area with physical characteristics which prevent effective exploitation of the population. It is also possible that an intensive fishery selects for behavioral traits which reduce the probability of capture in passive gear (e.g. traps) for some segment of the population. It is not currently possible to disprove any of the competing hypotheses with available information. A systematic approach to testing alternative hypotheses is required.

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## References

ANTHONY, V. C. 1980. Review of lobster mortality estimates in the United States. Can. Tech. Rep. Fish Aquat. Sci. 932: 17–25.

BEDDINGTON, J. R., AND J. G. COOKE. 1983. The potential yield of fish stocks. FAO Fish. Tech. Pap. 242: 47 p.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. Lond. Ser. 2: 519 p.

BOTERO, L., AND J. ATEMA. 1982. Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. J. Crustacean Biol. 2: 59–69.

BOTSFORD, L. W. 1984. Effect of individual growth rate on expected behavior of the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 41: 99–107.

BOTSFORD, L. W., AND D. E. WICKHAM. 1975. Correlation of upwelling index and Dungeness crab catch. Fish Bull. U.S. 73: 901–907.

1978. Behavior of age-specific, density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. 35: 833–843.

BULMER, M. G. 1975. The statistical analysis of density dependence. Biometrics 31: 901–911.

CADDY, J. F. 1979. The influence of variations in the seasonal temperature regime on survival of larval stages of the American lobster (*Homarus americanus*) in the southern Gulf of St. Lawrence. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 175: 204–216.

CAFFEY, H. M. 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. Ecol. Monogr. 55: 313–332.

CAMPBELL, A. 1980. A review of mortality estimates of lobster populations in the Canadian Maritimes. Can. Tech. Rep. Fish. Aquat. Sci. 932: 28–35.

CAMPBELL, A., AND J. BRATTEY. 1986. Egg loss from the American lobster, *Homarus americanus*, in relation to nemertean, *Pseudocarcinomertes homari*, infestation. Can. J. Fish. Aquat. Sci. 43: 772–780.

COBB, J. S. 1968. Delay of moult by the larvae of *Homarus americanus*. J. Fish. Res. Board Can. 25: 2251–2253.

1971. The shelter related behavior of American lobster, *Homarus americanus*. Ecology 52: 108–115.

COOPER, R. A., AND J. R. UZMANN. 1980. Ecology of juvenile and adult *Homarus*, p. 97–142. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY. 390 p.

FOGARTY, M. J. 1983. Distribution and relative abundance of American lobster, *Homarus americanus*, larvae: a review. NOAA Tech. Rep. NMFS SSRF 775, Washington, DC. p. 3–8.

GARROD, D. J. 1982. Stock and recruitment — again. Fish. Res. Tech. Rep. Dir. Fish. Res. Lowestoft 68: 1–22.

1983. On the variability of year class strength. J. Cons. Int. Explor. Mer 41: 63–66.

HANCOCK, D. A. 1973. The relationship between stock and recruitment in exploited invertebrates. Rapp. P-V. Reun. Cons. Int. Explor. Mer 164: 113–131.

HARRIS, J. G. K. 1975. The effect of density-dependent mortality in the shape of the stock and recruitment curve. J. Cons. Int. Explor. Mer 36: 144–149.

HAZLETT, B. A. 1983. Parental behavior in decapod crustacea, p. 171–198. *In* S. Rebach and D. W. Dunham [ed.] Studies in adaptation. The behavior of higher Crustacea. John Wiley & Sons, New York, NY.

HENNEMUTH, R. C., J. E. PALMER, AND B. E. BROWN. 1980. A statistical description of recruitment in eighteen selected fish stocks. J. Northw. Atl. Fish. Sci. 1: 101–111.

HUGHES, J. T., AND G. C. MATTHIESSEN. 1962. Observations on the biology of the American lobster, *Homarus americanus*. Limnol. Oceanogr. 7: 414–421.

JOLICOEUR, P. 1975. Linear regressions in fishery research: some comments. J. Fish. Res. Board Can. 32: 1491–1494.

LOOSANOFF, V. L. 1964. Variations in time and intensity of setting of the starfish, *Asterias forbesi*, in Long Island Sound during a twenty-five year period. Biol. Bull. (Woods Hole) 126: 423–439.

1966. Time and intensity of setting of the oyster, *Crassostrea virginica*, in Long Island Sound. Biol. Bull. (Woods Hole) 130: 211–227.

MCKELVEY, R., D. HANKIN, K. YANOSKO, AND E. SNYGG. 1980. Stable cycles in multi-stage recruitment models: an application to the northern California Dungeness crab (*Cancer magister*) fishery. Can. J. Fish. Aquat. Sci. 37: 2323–2345.

MORGAN, G. R., B. F. PHILLIPS, AND L. M. JOLL. 1982. Stock and recruitment relationships in *Panulirus cygnus*, the commercial rock (spiny) lobster of western Australia. Fish. Bull. U.S. 80: 475–486.

PALOHEIMO, J. E. 1963. Estimation of catchabilities and population sizes of lobsters. J. Fish. Res. Board Can. 20: 59–88.

PAULIK, G. J. 1973. Studies of the possible form of the stock–recruitment curve. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 164: 302–315.

PENN, J. W., AND N. CAPUTI. 1985. Stock recruitment relationships for the tiger prawn, *Penaeus esculentus*, fishery in Exmouth Gulf, Western Australia, and their implications for management, p. 165–173. *In* P. C. Rothlisberg, B. J. Hill, and D. J. Staples [ed.] Second Australian National Prawn Seminar.

PETERMAN, R. M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. Can. J. Fish. Aquat. Sci. 38: 1113–1119.

REEVES, J. E. 1982. Data requirements for tanner crab management, as suggested by the Bristol Bay king crab management model. Proc. Int. Symp. on the genus *Chionoecetes*. Alaska Sea Grant Rep. No. 82-10: 732 p.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

1973. Linear regressions in fishery research. J. Fish. Res. Board Can. 30: 409–434.

ROBINSON, D. G. 1979. Consideration of the lobster (*Homarus americanus*) recruitment overfishing hypothesis with special reference to the Canso Causeway. Fish. Mar. Ser. Tech. Rep. 834: 78–99.

SCARRATT, D. J. 1964. Abundance and distribution of lobster lavae (*Homarus americanus*) in Northumberland Strait. J. Fish. Res. Board Can. 21: 661–680.

1973. Abundance, survival, and vertical and diurnal distribution of lobster larvae in Northumberland Strait, 1962–63, and their relationships with commercial stocks. J. Fish. Res. Board Can. 30: 1819–1824.

SEIGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, NY.

SISSENWINE, M. P. 1984. Why do fish populations vary? p. 59–109. *In* R. May [ed.] Exploitation of marine communities. Springer-Verlag, Berlin.

SLADE, N. A. 1977. Statistical detection of density dependence from a series of sequential censuses. Ecology 58: 1094–1102.

SOKAL, R. F., AND F. J. ROHLF. 1981. Biometry. 2nd ed. W. H. Freeman and Co., San Francisco, CA.

STAPLES, D. J. 1985. Modelling the recruitment processes of the banana prawn, *Penaeus merguinsis*, in the southeastern Gulf of Carpentaria, Australia, p. 175–184. *In* P. C. Rothlisberg, B. J. Hill, and D. J. Staples [ed.] Second Australian National Prawn Seminar.

SUTCLIFFE, W. H. JR. 1973. Correlations between seasonal river discharge and local landings of American lobster (*Homarus americanus*) and Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence. J. Fish. Res. Board Can. 30: 856–859.

TANG, Q. 1985. Modification of the Ricker stock recruitment model to account for environmentally induced variation in recruitment with particular reference to the blue crab fishery in Chesapeake Bay. Fish. Res. 3: 13–21.

WILBUR, H. M. 1980. Complex life cycles. Annu. Rev. Ecol. Syst. 11: 67–93.

WILDER, D. G. 1953. The growth rate of the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 10: 371–412.

1963. Movements, growth, and survival of marked and tagged lobsters liberated in Egmont Bay, Prince Edward Island. J. Fish. Res. Board Can. 20: 305–318.

## Appendix

A simple model for density-independent growth is given by the differential equation

$$dN/dt = aN$$

where $a$ is the instantaneous rate of population growth and $N$ is

population size. This equation may be rewritten

$$(1/N)\, dN/dt = d \ln N/dt = a.$$

The solution may be expressed

$$\ln N_{t+r} = a(t - t_0) + \ln N_t.$$

Note that if we have a time series of population estimates, we can fit this model by regressing $\ln N_{t+r}$ on $\ln N_t$. The intercept will be an estimate of $a(t - t_0)$ and the expected slope is 1.0 (note that the implied coefficient for the term $\ln N_t$ is 1.0). Therefore, we may compute the regression estimates and test the null hypothesis that the slope does not differ significantly from 1.0. If we accept the null hypothesis, we conclude that the density-independent population model cannot be rejected.

# Session 9
# Implications of the Workshop

# Summary of Session 2: Lobster Fisheries and Recruitment Variability

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The mandate of this session was threefold: to highlight recruitment variability; to document perceived biotic and abiotic causes of this variability; and to outline current understanding of lobster/crab stock–recruitment relationships. Delegates from countries as geographically distant as Brazil and New Zealand, and as politically distant as Cuba and the United States, presented data from their respective fisheries.

All session delegates presented, or had access to, long-term annual catch data. Where hundreds (the Western Australian rock lobster (*Panulirus cygnus*) fishery; see Caputi and Brown, this issue; Phillips, this issue) to thousands (eastern Canadian American lobster (*Homarus americanus*) fishery; see Ennis, this issue) of fishermen are involved, the collection and collation of accurate data is no small task.

Significant annual variation was evident in the catch data presented for crab and spiny and clawed lobster. For example, Ennis (this issue) demonstrated that certain American lobster stocks exhibit only minor fluctuations in annual abundance. Others, however, under similar management regimes, oscillated wildly and ultimately collapsed. Jamieson (this issue) disclosed a similar phenomenon for both the northern Pacific Dungeness crab (*Cancer magister*) and *Chionocetes* spp. (Tanner and snow crab) fisheries. Overall, annual landings tended to fluctuate ≤30%; however, the oscillation range increased markedly at the peripheries of commercial abundance.

The geographic patterns of annual landings for the Florida spiny lobster (*Panulirus argus*) were similar to that of the Dungeness crab. The landings of *P. argus* at the southern (e.g. Brazil (A. Fonteles-Filho, Professor of Fisheries Science, Universidade Federal do Ceara, Fortaleza, Brazil, pers. comm.)) and northern (e.g. Florida (Lyons, this issue)) extremes of commercial abundance have decreased markedly whereas in the center of the distribution (e.g. Cuban fishery (J. A. Baisre, Fisheries Biologist, Centro de Investiqueions Pesquera, Havana, Cuba, pers. comm.)), landings exhibited only minor annual fluctuations.

The South African western rock lobster (*Jasus lalandii*) fishery extends 900 km from Cape Town to the Orange River (Pollock, this issue). Although only minor annual landing fluctuations occur, there has been a marked 25-yr decline in annual catch, from 10 000 to 3500 t. Drastic management measures were implemented in both the extreme north and south; the latter fishery responded; the former fishery did not.

The Western Australia rock lobster fishery also exhibits annual landing fluctuations (Caputi and Brown, this issue; Phillips, this issue). For example, between 1964 and 1968 the fluctuations ranged by 25%. However, unlike any of the above fisheries, between 1972 and 1982 annual landings doubled.

Expenditures to acquire accurate and timely annual catch data in decapod crustacean fisheries, although high, are probably less than expenditures required to permit an understanding of the causes of these fluctuations. Ideally, the first step is to understand the stock–recruitment relationships of each fishery. This, in all but the Western Australian rock lobster fishery (Phillips 1981), appears to be an enigma, as pointed out by Hancock (1980) at the first lobster workshop: "The relationship between stock and recruitment, which may be of fundamental importance to successful management has . . . proved to be one of the most difficult to quantify." The key to discerning *P. cygnus* stock–recruitment was an understanding of larval natural history. Without knowledge of the life history stages, stock assessment analyses are often meaningless. As well, attempts at understanding the underlying mechanisms responsible for annual catch fluctuations frequently involve indirect techniques such as correlations. For example, numerous hypotheses, including both wind direction and sunspot activity during zoeal stage, have been developed to account for northern California Dungeness crab abundance cycles (Jamieson, this issue). Similarly, since 1979, four hypotheses have been developed to account for annual landing cyclicity and stock collapse of the American lobster fishery along oceanic Nova Scotia (Ennis, this issue). One of Jamieson's (this issue) conclusions derived from the Dungeness crab review is appropriate here: "The main concensus is, that additional biological study in the field is needed if resolution of causative mechanisms is ever to be achieved."

Certain countries include the opinion of fishermen in resource management decisions. Fishermen often demand sound data on source of recruitment before consenting to measures on conservation of brood stock. Management action for both the Florida spiny lobster fishery (Lyons, this issue) and the northwestern Atlantic American lobster fishery (Pringle et al. 1983) is at a standstill for want of these data. By contrast, the Cuban *P. argus* fishery resource managers (J. A. Baisre, pers. comm.) claim a stock–recruitment relationship for their lobster fisheries. This gave them the confidence, when 1978 annual landings decreased markedly, to introduce remedial measures. The fishery has rebounded.

The concept of life history "critical stage" was broached by Jamieson (this issue). He gave evidence that perturbations of both larval and juvenile stages influence crab recruitment. The critical stage in the life history of *P. cygnus* would appear to be the larvae, at least between 1969 and 1982. Phillips (this issue) demonstrated a relatiely close relationship between puerulus abundance on collectors and annual catches 4 yr later. As well, Caputi and Brown (this issue) showed a positive relationship between the incidence of trap-caught "shorts" (sublegals) and landings of "whites" (the *P. cygnus* first-year recruits). They state "... there appears to be no evidence of environmental

factors strongly affecting recruitment after the juvenile stage. . ."

The Hawaiian *P. marginatis* fishery is in the development stage. Nevertheless, agencies have funded assessment science. MacDonald (this issue) noted annual and regional shifts in annual puerulus abundance on settlement collectors. He matched these variances to major oceanographic current shifts. Given powerful currents ($>50\ m \cdot s^{-1}$), it appears that the population may be recruitment limited. Juvenile nursery grounds, in contrast with *P. cygnus* distribution, are not separate from brood-stock areas.

There is little doubt that the most outstanding crustacean decapod resource management success story is that of the Western Australian rock lobster fishery. There appears to have been a sound marriage between all sectors of resource management: assessment science, economics, sociology, resource development, and enforcement. We know that there is more to successful resource management than good science (Pringle 1985). For example, Rhys Brown spends many hours annually packaging good science and presenting it to industry representatives.

Scientific resource management is a concept touted by many agencies but practiced by few (Watt 1968). First, a suitable resource management structure must be in place; and secondly, excellent scientific leadership is required to keep research personnel target oriented. These must have been in place early in the exploitation history of the Western Australian rock lobster fishery. Sheard (1949), for example, was doing phyllosome ecology before mid-century. As a result of this fine work a system is now in place that permits recruit prediction 2–4 yr in advance. The costs are small; resource management costs are only 2.5% of the gross landed value ($A93.1 million), and annual research costs are a mere 21% of resource management costs.

The "good news" is that the rest of us have a success story to emulate. The "bad news" is that the *P. cygnus* fishery is simple politically (one country and one state) compared with most lobster fisheries. Compare this with the Florida spiny lobster fishery that transcends both the Gulf of Mexico and the Caribbean.

We have come a long way in fisheries science, a very complex discipline. It is little wonder that the many threads that tie, say a lobster brood stock to fishery recruits, have rarely been unravelled. We frequently forget that ecology is a relatively new science: it was only 120 yr ago that Ernst Haekel coined the term "ecology" (Mayre 1982); it was only the American midwest dustbowl of the 1930's that united the conservation concept with the discipline of ecology (Worster 1977).

## References


HANCOCK, D. A. 1980. Introduction. Part II. Management, p. 181–188. *In* J. S. Cobb and B. F. Phillips [ed.]. The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

MAYRE, E. 1982. The growth of biological thought. Harvard University Press, Cambridge, MA.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

PRINGLE, J. D. 1985. The human factor in fishery resource management. Can. J. Fish. Aquat. Sci. 42: 389–392.

PRINGLE, J. D., D. G. ROBINSON, G. P. ENNIS, AND P. DUBÉ. 1983. An overview of the management of the lobster fishery in Atlantic Canada. Can. MS Rep. Fish. Aquat. Sci. 1701: 103 p.

SHEARD, K. 1949. The marine crayfish (spiny lobster), family Palinuridae, of Western Australia. Aust. Comm. Sci. Res. Org. Bull. 247: 1–45.

WATT, K. E. F. 1968. Ecology and resource management. McGraw-Hill Book Company, Toronto, Ont.

WORSTER, D. 1977. Natures economy. A history of ecological ideas. Cambridge University Press, New York, NY.

# Summary of Session 3: Larval Distribution Dynamics

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It is usual for a chairman to review and attempt to draw conclusions from the papers presented at a workshop. Instead, I should like to discuss some of the problem areas in larval distribution research: areas we have neglected, areas for which we have inadequate data, areas where research should or might be concentrated.

## Identification of the Larvae

Phyllosomata larvae, particularly the early stages, are still difficult to identify in most species. It is not possible, for example, to distinguish the early stage phyllosomata of the western Atlantic species *Panulirus argus (Latreille), P. guttatus* (Latreille), and *P. laevicauda* (Latreille) from one another (Lyons and Little 1975); however, the later stages of *P. laevicauda* have been distinguished from *P. argus* (Baisre and de Quevedo 1982). The literature also contains many drawings and descriptions of larvae of unknown species (e.g. Johnson 1951, 1968a, 1968b; Sims 1964; Baez 1973; Phillips et al. 1981). The significance of the problem is illustrated further by Lesser (1974), who demonstrated that the criteria used by a number of earlier workers in several areas around the world were unreliable in distinguishing between the larvae of the Scyllaridae and the Palinuridae.

Identification could be achieved by cultivating larvae or by collecting larvae from the field and rearing them until they metamorphosed into identifiable puerulus and/or benthic stages. However, an alternative approach is available. Multivariate numerical methods and discriminant analysis techniques of the morphometrics of specimens have been used successfully to determine the species of the larvae of Penaeid shrimp with high accuracy (Rothlisberg et al. 1983). Rothlisberg worked with a complete series of stages of each species, which is not yet available for the panulirid species. However, it remains only to apply such techniques to the phyllosomata larvae, which would almost certainly lead to the distinguishing of additional characteristics useful in the separation of the larvae, and eventually in the identification of missing stages.

## Vertical Migration

The vertical movement of few species has been documented, although Phillips et al. (1978) and Phillips et al. (1981) have shown that these movements are critical in the larval transport processes of *Panulirus cygnus* George and *Scyllarus bicuspidatus* (De Man).

In all, 48 species of the Palinuridae have been recognized (Phillips and Sastry 1980). Of these, the vertical migration behaviour of the phyllosoma larvae have been studied in only *P. cygnus*, *S. bicuspidatus* (Phillips et al. 1981), and *P. argus* (Austin 1972), with some incidental data on *Jasus edwardsii* (H. Milne-Edwards) (Booth 1980). The studies found clear differences in behaviour, but the work has yet to be extended to the pueruli, although they probably also have vertical migration patterns.

The importance of obtaining vertical migration data cannot be overemphasized. As the advection distance and larval direction likely change with larval development, sampling should be designed to take this into account. Tidal transport, where applicable, should be studied as well for selective transport. Current speed and direction must be measured simultaneously and analysed in conjunction with data on the vertical distribution of the larvae.

## Sampling Techniques

Because of the behaviour of the phyllosomata larvae, the mid- and late stages are not found at the surface except when moonlight illuminance is low (Rimmer and Phillips 1979). Consequently, it is important to record light levels when sampling.

From examination of the density of larvae in oceanic waters, it is apparent that phyllosomata and pueruli are rare animals in plankton (Lazarus 1967; Johnson 1974). Sampling by drop-net or vertical haul will not, therefore, give a clear indication of the presence or absence of larvae, since these techniques do not sample a sufficient volume of water.

A better approach is to use multisampling systems such as Mocness (Wiebe et al. 1976) or BIONESS (Sameoto et al. 1980) which permit large-volume, sequential samples and also enable environmental data to be collected simultaneously.

We also need to develop a technique for catching phyllosomata larvae undamaged so we can determine how and at what speeds phyllosomata swim and also how they react to various stimuli, especially what causes vertical movements. The behaviour of mid- and late-stage larvae might be observed in the field using SCUBA or a submersible.

## Ocean Circulation

Details of the circulation of the ocean generally are not available on the scale that is needed for the kinds of analyses that would produce any real understanding of larval advection. This is particularly a problem with the currents of the upper 300 m of the water column. Satellite tracking buoys can provide detailed data on some water movements, although their design can be such that the data obtained are severely limited. For example, the drogue attached to the buoy is usually about 20 m below the surface. It therefore gives a measure of the water movements at that level, but not at all levels through which the phyllosomata larvae are moving vertically.

The above criticism was dismissed by Thorson (1961) with the argument that the movements of the upper 300 m of the

water column tend to be alike throughout the depth strata. However, the drogues are deliberately set well *below* the surface to avoid the effects of surface currents generated by the wind, and the data indicate that it is in these currents that the early phyllosoma larvae of *P. cygnus* are transported offshore. They pass over the top of and move in the opposite direction to the easterly movement of the upper 300 m of the southeastern Indian Ocean (Phillips 1981).

The absence of described water movements may be the result of inadequate data, lack of investigation, or inability to detect the flow by the usual physical methods. New water movements are constantly being described. For example, the subtropical countercurrent extending from the western boundary of the Pacific to near the Hawaiian Islands was predicted from a theoretical study by Robinson (1968) but was not confirmed until 1978 (Hasunuma and Yoshida 1978). The presence of the phyllosomata larvae of *Panulirus longipes femoristriga* (von Martens) and *Scyllarus demani* Holthuis in the waters off Hawaii (B. F. Phillips and P. S. McWilliam, unpubl. data) provides further evidence of the existence of the current.

Data from satellite studies are being used extensively to improve our understanding of ocean circulations. However, such data must be interpreted carefully, preferably in collaboration with physical oceanographers.

## Future Research

At present it is not possible to determine the place of origin of the larvae that eventually survive and settle, for they have been subject to unknown circulatory features. Yet, as pointed out by Idyll (1981), this is a vital issue because management cannot be fully efficient until it is known whether adjacent lobster stocks are connected, separate, or somewhere between these extremes.

Can we substantially improve our understanding of larval transport processes and ocean circulation features? Further progress will certainly be both difficult and expensive. The scale of larval distribution imposes tremendous problems in developing a real-time picture of larval distributions and of the circulations on which distributions depend. Sampling from ships does not appear to be a solution.

Although technology has developed enormously in recent years, it is not yet possible to tag an animal that develops from a larva the size of a pinhead through a series of moults to 10 cm long and then metamorphoses into a puerulus or nisto stage before settlement. Radioactive tracers are not yet practical, and biochemical approaches have proved inconclusive, partly because of the lower genetic variability of crustaceans (Hedgecock et al. 1977; Hedgecock and Nelson 1980; Mulley and Latter 1980; Redfield et al. 1980; Menzies 1981; Shaklee and Samollow 1984; Salini et al. 1986). Mitochondrial DNA has been cited as a possible means of identifying populations (Lyons, this issue) but the technique probably is some years away from fruition.

The development of drogues or satellite-tracked buoys that simulate the circadian vertical migration of larvae should be investigated. They, combined with such innovations in satellite oceanography as the microwave scatterometer that is used aboard SEASAT-A to estimate wind stress at a resolution of 50 km, may provide some solutions. Even though the advection, diffusion, and drift migration of larval fish have been the subject of many studies, most researchers would agree with Power (1984) that diffusion of fish larvae in the sea is not yet understood. Also, we are a long way from understanding these processes in spiny lobster larvae.

The successful culturing of phyllosomata larvae throughout their complete development would fill a serious gap in our knowledge. Special attention was paid to this area in the 1960s and 1970s. There have been some impressive achievements with scyllarids including *Scyllarus americanus* (Smith) by Robertson (1968), *Ibacus ciliatus ciliatus* (von Siebold) and *Ibacus novemdentatus* Gibbes by Takahashi and Saisho (1979), *Ibacus alicronatus* Bate by Atkinson and Boustead (1982), *Thenus orientalis* (Lund) by Barnett et al. (1984) and Masahiro Ito (James Cook University of North Queensland, Australia, pers. comm.), and *Scyllarus kitanoviriosus* by Higa and Saisho (1983). Inoue (1978) reported the rearing of the phyllosoma larvae of *P. japonicus* up to the last phyllosoma stage. However, examination of the illustration of this last stage shows that it does not possess gills, and so it is possible that it may not be the final phyllosoma stage of this species. Certainly no palinurid species has been cultured through its larval development to metamorphosis into the puerulus stage and few attempts have been made for almost 10 yr. Jiro Kittaka (Kitasato University, Japan, pers. comm.) is currently attempting to culture *Jasus* sp. through its larval development.

A major difficulty is that the diet of the different larval stages is not known. One approach to this problem would be to study the natural diet. The structure of the mouthparts and thoracic appendages suggests that phyllosoma larvae are best adapted to capturing and eating large, soft-bodied forms such as medusae. Several workers (including Shojima 1963; Thomas 1963; Herrnkind et al. 1976) have found the phyllosomata larvae of a number of Scyllaridae (but not Palinuridae) clinging to certain hydrozoan and scyphozoan medusae. Sims and Brown (1968) reported undigested nematocysts in fecal material from a specimen of a scyllarid phyllosomata. These observations suggest that larval food may be relatively liquid in form, which would explain the absence of food particles in the gut. An immunological approach, as used successfully to investigate diets of spiders in orchards, is a possibility. The recent development of rapid methods of characterising organic compounds such as NMR and chromatographic techniques offer possible solutions.

Most of my comments have been directed chiefly towards the study of palinurids although they apply generally to crab and clawed lobster studies. However, I will end with a comment on *Homarus americanus* H. Milne-Edwards. The successful development of a multiyear predictive system for *P. cygnus* in Australia suggests that it would be feasible to develop a similar system for *H. americanus*.

## References


ATKINSON, J. M., AND N. C. BOUSTEAD. 1982. The complete larval development of the scyllarid lobster *Ibacus alticrenatus* Bate, 1888, in New Zealand waters. Crustaceana 42(3): 275–287.

AUSTIN, H. M. 1972. Notes on the distribution of phyllosoma of the spiny lobster *Panulirus* spp., in the Gulf of Mexico. Proc. Nat. Shellfish Assoc. 62: 26–30.

BAEZ, P. R. 1973. Larvas phyllosoma del pacifico sur oriental (Crustacea:Macrura:Scyllaridae). Rev. Biol. Mar. Valparaiso 15(1): 115–130.

BAISRE, J. A., AND M. E. R. DE QUEVEDO. 1982. Two phyllosoma larvae *Panulirus laevicauda* (Latreille, 1817) (Decapoda:Palinuridae) from the Caribbean Sea with a discussion about larval groups within the genus. Crustaceana 43(2): 147–153.

BARNETT, B. M., R. F. HARTWICK, AND N. E. MILWARD. 1984. Phyllosoma and nisto stage of the Morton Bay Bug, *Thenus orientalis* (Lund) (Crus-

tacea:Decapoda:Scyllaridae), from shelf waters of the Great Barrier Reef. Aust. J. Mar. Freshwater Res. 35: 143–152.

BOOTH, J. D. 1980. Larval recruitment studies. Catch '80, 7(7): 22–23.

HASUNUMA, K., AND K. YOSHIDA. 1978. Splitting of the subtropical gyre in the western North Pacific. J. Oceanogr. Soc. Jpn. 34: 160–172.

HEDGECOCK, D., AND K. NELSON. 1980. Enzyme polymorphism and adaptive strategy in the decapod crustacea. Am. Nat. 116: 238–280.

HEDGECOCK, D., K. NELSON, J. SIMONS, AND R. SHLESER. 1977. Genetic similarity of American and European species of the lobster *Homarus*. Biol. Bull. 152: 41–50.

HERRNKIND, W. F., J. HALUSKY, AND P. KANCIRUK. 1976. A further note on phyllosoma larvae associated with medusae. Bull. Mar. Sci. 26: 110–112.

HIGA, T., AND T. SAISHO. 1983. Metamorphosis and growth of the late-stage phyllosoma of *Scyllarus kitanoviriosus* Harada (Decapoda, Scyllaridae). Mem. Kiagoshima Univ. Res. Cent. S. Pac. 3(2): 86–98.

INOUE, M. 1978. Studies on the cultured phyllosoma larvae of the Japanese spring lobster, *Panulirus japonicus*. Bull. Jpn. Soc. Sci. Fish. 44: 457–475.

IDYLL, C. P. 1981. Summary and importance of the GCF1 sessions on spiny lobsters. Proc. Gulf Caribb. Fish. Inst. 33: 322–335.

JOHNSON, M. W. 1951. A giant phyllosoma larva of loricate crustacean from the tropical Pacific. Trans. Am. Microsc. Soc. 70: 274–278.

1968a. Palinurid phyllosoma larva from the Hawaiian Archipelago (Palinuridae). Stud. Decapod Larv. Develop. Crustaceana (Suppl.) 2: 59–79.

1968b. On phyllamphion larvae from the Hawaiian Islands and the South China Sea (Palinuridae). Crustaceana (Suppl.) 2: 38–46.

1974. On the dispersal of lobster larvae into the east Pacific barrier (Decapoda, Palinuridae). Fish. Bull. 72: 639–647.

LAZARUS, B. I. 1967. The occurrence of phyllosoma off the cape with particular reference to *Jasus lalandii*. S. Afr. Div. Sea Fish. Invest. Rep. 63.

LESSER, J. H. R. 1974. Identification of early larvae of New Zealand spiny and shovel-nosed lobsters (Decapoda, Palinuridae, Scyllaridae). Crustaceana 27: 259–277.

LYONS, W. G., AND E. J. LITTLE. 1975. Problems and potentials of research on phyllosoma larvae of Florida spiny lobsters, p. 7–8. *In* W. Seaman and A. C. Jones [ed.] Review of spiny lobster research, including results and recommendations of a colloquium held October 1 and 2 in Miami, FL (and) summaries of current research projects in Florida. Florida Sea Grant, Gainesville, FL.

MENZIES, R. A. 1981. Biochemical population genetics and the spiny lobster larval recruitment problem: an update. Proc. Gulf Caribb. Fish. Inst. 33: 207–229.

MULLEY, J. C., AND B. D. H.LATTER. 1980.Genetic variation and evolutionary relationships within a group of 13 species of penaeid prawns. Evolution 34: 904–916.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

PHILLIPS, B. F., P. A. BROWN, D. W. RIMMER, AND S. J. BRAINE. 1981. Description, distribution and abundance of late larval stages of the Scyllaridae (slipper lobsters) in the southeastern Indian Ocean. Aust. J. Mar. Freshwater Res. 32: 417–437.

PHILLIPS, B. F., D. W. RIMMER, AND D. D. REID. 1978. Ecological investigations of the late stage phyllosoma and puerulus larvae of the western rock lobster *Panulirus longipes cygnus*. Mar. Biol. 45: 347–357.

PHILLIPS, B. F., AND A. N. SASTRY. 1980. Chapter 7. Larval ecology p. 11–57. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Ecology and management. Academic Press, New York, NY.

POWER, J. H. 1984. Advection, diffusion, and drift migration of larval fish, p. 27–37. *In* J. D. McCleave, G. P. Arnold, J. J. Dodson, and W. H. Neil [ed.] Mechanisms of migration in fishes. Ser. V. Marine sciences. NATO Conf. Series.

REDFIELD, J. A., D. HEDGECOCK, K. NELSON, AND J. P. SALINI. 1980. Low hereozygosity in tropical crustaceans of Australia and the trophic stability hypothesis. Mar. Biol. Lett. 1: 303–313.

RIMMER, D. W., AND B. F. PHILLIPS. 1979. Diurnal migration and vertical distribution of phyllosoma larvae of the western rock lobster, *Panulirus cygnus* George. Mar. Biol. 54: 109–124.

ROBERTSON, P. B. 1968. The complete larval development of the sand lobster, *Scyllarus americanus* (Smith) (Decapoda, Scyllaridae) in the laboratory, with notes on larvae from the plankton. Bull. Mar. Sci. 18: 294–342.

ROBINSON, M. K. 1968. Theoretical predictions of subtropical countercurrent confirmed by bathythermograph (BT) data. Bull. Jpn. Soc. Fish. Oceanogr. Spec. No. (Professor Uda's Commemorative Papers): 115–121.

ROTHLISBERG, P. C., C. J. JACKSON, AND R. C. PENDREY. 1983. Specific identification and assessment of distribution and abundance of early penaeid shrimp larvae in the Gulf of Carpentaria, Australia. Biol. Bull. 164: 279–298.

SALINI, J., G. RINTOUL, J. B. SHAKLEE, AND B. PHILLIPS. 1986. An electrophoretic analysis of stock structure in the ornate tropical rock lobster, *Panulirus ornatus*, p. 218–232. *In* A. K. Haines, G. C. Williams, and D. Coates [ed.] Torres Strait Fisheries Seminar, Port Moresby, 11–14 February 1985. Aust. Fish. Serv. Aust. Govt. Publ. Serv., Canberra.

SAMEOTO, D. D., L. O. JAROSZYNSKI, AND W. B. FRASER. 1980. BIONESS, a new design in multiple net zooplankton samplers. Can. J. Fish. Aquat. Sci. 37: 722–724.

SHAKLEE, J. B., AND P. B. SAMOLLOW. 1984. Genetic variation and population structure in a spiny lobster, *Panulirus marginatus*, in the Hawaiian Archipelago. Fish. Bull. 82(4): 693–702.

SHOJIMA, Y. 1963. Scyllarid phyllosoma's habit of accompanying jellyfish. Bull. Jpn. Soc. Sci. Fish. 29: 349–353.

SIMS, H. W. JR. 1964. Four giant scyllarid phyllosoma larvae from the Florida Straits with notes on smaller similar specimens. Crustaceana 7(4): 259–266.

SIMS, H. W. JR. AND C.L. BROWN. 1968. A giant scyllarid phyllosoma larva taken north of Bermuda (Palinuridae). Crustaceana (Suppl.) 2: 80–82.

TAKAHASHI, M., AND T. SAISHO. 1979. The complete larval development of the scyllarid lobster, *Ibacus ciliatus* (von Siebold) and *Ibacus novemdentatus* Gibbes, in the laboratory. Mem. Fac. Fish. Kagoshima Univ. 27(1): 305–353.

THOMAS, L. 1963. Phyllosoma larvae associated with medusae. Nature (Lond.) 198: 208.

THORSON, G. 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents, p. 455–474. *In* Oceanography. American Association for the Advancement of Science, Washington, DC.

WIEBE, P. J., K. H. BURT, S. H. BOYD, AND A. W. MORTON. 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34: 313–326.

# Summary of Session 4: Behavior and Movements

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International workshops are expected to strongly and positively influence the direction of research thereafter and to promote future advances in the state of knowledge. At this time, it seems instructive to recall the status of knowledge of lobster movements and behavior at the 1977 U.S.–Australian Workshop on clawed and rock lobsters (Phillips and Cobb 1977) and to evaluate progress based upon the presentations in the 1985 Workshop. My assessment in 1977, regarding spiny lobster movement patterns, was that migrations were inadequately characterized for most species and environmental regulating factors were uncertain (Herrnkind 1980). According to Atema and Cobb (1980), detailed studies of lobster behavior were rare and the role of social behavior in lobster ecology and population reproductive patterns was essentially unstudied. Phillips and Sastry (1980) noted that natural microhabitats of settling spiny lobster pueruli and *Homarus* larvae were rarely known and the behavioral ecology of the postlarval and early benthic period unexplained. Each of the above workers, among others, recommended certain research directions and proposed methodological improvements needed to solve the problems.

Migration researchers called for a "tightening" of tag–recapture methods to reduce interpretive bias and suggested that research be designed around a hypothesis-testing framework. The studies reported here by Campbell (this issue), P. Daniel, R. Bayer, and J. Krouse (pers. comm.), Pezzack and Duggan (this issue), and T. L. Meyer, J. R. Uzmann, R. A. Cooper, and M. J. Fogarty (pers. comm.) clearly show that the suggested approaches are now state-of-the-art. Tag–recapture programs on *Homarus americanus* are critically assessed and biases in collection accommodated. Hypothetical questions are stated and clear from the tagging plan and data analysis, e.g. the common focus on inshore–offshore movement in respect to season, reproduction, and temperature. Campbell (this issue) created an environment for fruitful followup questions by proposing that female movements function as a thermal adjustment enhancing egg development. Booth (this issue) provided evidence for a direct recruitment function in the New Zealand packhorse lobster, *Jasus verreauxi*, which is proposed to migrate contranatantly to spawn, thereby sustaining the life cycle in a warm environment. Overall, the vague scatters of returns that typified migration studies of the past are now being replaced by directional arrows.

Ethologists in 1977 recommended long-term, detailed study in "naturalistic" conditions as the only reasonable way to routinely visualize lobster behavior. In addition, they called for corroboration and synthesis with available field information. The study by Atema (this issue) exemplified just this approach, showing that the localized movements of *H. americanus* constitute a pattern of sociality tied directly to courtship and mating. We must now perceive the lobster as a complex social animal on a level with lower vertebrates and mammals. R. N. Lipcius (pers. comm.) tied together several serendipitous observations based on a long-term naturalistic study designed from field situations of *Panulirus argus*. The use of different aged individuals, ranging from subadult to long-mature, led him to propose an age-dependent pattern of palinurid reproduction and reproductive timing, functionally linked to larval development and eventual postlarval recruitment. Work such as this demonstrates the potential of behavioral research for discovering principles of large-scale significance, many of which are of fishery interest. Two previous directives for research on postlarval behavior and ecology had apparent impact: (1) find the natural settlement habitats and (2) use reared *Homarus* and collector-trapped *Panulirus* postlarvae for intensive study. Numerous papers in Session 3 (this issue) and Cobb's paper presented at the Workshop in Session 4 provide evidence for a large commitment to the latter approach to *H. americanus*. Marx (this issue) combined both approaches to discover the essential conditions for settlement and early benthic life of *P. argus*. A microhabitat providing shelter from predators and environmental perturbations, while supplying a continuous food source, may be a general phenomenon for palinurids. The fact that this type of microhabitat differs substantially from that of the later juvenile phase invites management considerations.

Much has been accomplished to date but it is now necessary to prophesize lobster research for the next decade. To that end, I make a tripartite recommendation centered around intensified "fine-grain" behavioral–ecological research on larvae, postlarvae, and early benthic stages, as well as on older stages. First, we should seek to delineate the causal linkage between environmental conditions and behavior, including movements. Second, we should seek to determine the mechanisms of internal regulation of behavior by endocrine processes. Third, we should seek further understanding of lobster sensory capabilities. In all of this, behavioral ecologists must attempt to extend their insights from the level of the individual organism to that of the population.

## References

ATEMA, J., AND J. S. COBB. 1980. Social behavior, p. 409–450. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

HERRNKIND, W. F. 1980. Spiny lobsters: patterns of movement, p. 349–407. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

PHILLIPS, B. F., AND J. S. COBB. 1977. Workshop on lobster and rock lobster ecology and physiology. Circ. CSIRO Div. Fish. Oceanogr. (Aust.) No. 7.

PHILLIPS, B. F., AND A. N. SASTRY. 1980. Larval ecology, p. 11–57. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

# Summary of Session 5: Recruitment Enhancement

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The usual approach for managing a fishery is to attempt to optimize the yield by adjusting the fishing regulations. The age or size at first capture, the fishing effort, or the amount harvested during a fishing season of defined duration can be modified at will by the manager. All these measures actually consist in modifying the fishing mortality, assuming that density-dependent effects on biological parameters such as growth, natural mortality, and recruitment are negligible. The incidence of a proposed management strategy on the fishery is modelled by a "dynamic pool" which almost never includes input for recruitment: in a "simple yield per recruit" model, it is assumed that within the range of management measures, the recruitment will remain constant.

Limited attempts are also frequently made to improve recruitment by maintaining or increasing the production of eggs. The usual approaches consist of defining fishing regulations protecting the egg-bearing females. Alternatively, a minimum legal size is impounded, either directly or by selectivity of fishing gear, in order to allow several spawnings before capture.

The theme of this session deals with a wide range of approaches related to recruitment enhancement. Some of them are traditional and are related to conservation of stocks by fisheries regulations such as protection of female; others are unconventional and are far more ambitious, involving directed actions to modify biological parameter rather than fishing. In the latter, attempts are made to promote the production of larvae and prerecruits, to enhance their growth, and to increase their survival.

This type of recruitment enhancement does not involve changes in fishery regulations; it is usually very appealing to the fishermen because they do not have to modify their fishing habits. The fishery managers, ideally, supplement mother nature by enhancing stock production so that fishermen may catch more.

The idea of recruitment enhancement is ancient. At the beginning of the century there was a frenzy for "restocking" the ocean by having various species of fish (cod, herring) or invertebrates (lobsters) spawn in hatcheries and multitudes of young larvae released at sea. Soon it became evident that the contribution of hatchery-produced larvae was negligible when compared with the natural production even for depleted stocks. It was observed that natural mortality of young larvae was extremely high in the natural environment. A few recruitment enhancement projects based on the release of larvae at sea are still being operated. Financing usually is provided through fishermen's organizations. Scientific surveys of subsequent recruitment to the fishery are either nonexistent or inconclusive.

Other early attempts to enhance recruitment include the increase of primary productivity by dumping nutrients in semi-closed lagoons or by throwing chopped trash fish, caught while trawling, back into low-productivity bodies of water. These approaches have not proved to be efficient.

Recently there has been a renewed interest in recruitment enhancement of lobsters. This has somehow been justified by the very limited success of more traditionally accepted fisheries management techniques. A considerable research effort has been developed for a better understanding of the early life history of homarid and palinurid lobsters mainly for aquaculture purposes of homarid but also for prediction of recruitment of palinurid lobsters. Thus far, the aquaculture attempts have not resulted in the establishment of any economical projects, but the techniques for mass production of young *Homarus* spp. now are well known (Hruby 1979). Laboratory production of young palinurids has been mostly unsuccessfull due to the duration of the phyllosoma stage (reported to extend up to 2 yr). However, collection in the wild and subsequent raising of individuals in the next stage, the puerulus, has met with some success (Booth 1979; Little and Milano 1980; Phillips 1985; Phillips and Hall 1978).

From such recent advances in the knowledge of life histories (Howard and Bennett 1979), methods have been proposed for enhancing production of eggs, of larvae, and of prerecruits by supplementing possible deficiencies in natural mechanisms affecting population densities or by modifying fishing techniques when sublegal-sized animals are being captured and released. These methods range from preservation to aquaculture, but they share a common link: the enhancement of recruitment to the fishery. I shall review some of these methods and briefly summarize the contributions of the participants to the session on recruitment enhancement on the following themes: (1) reducing fishery-induced mortality on prerecruits; (2) collecting and protecting young lobsters from the wild; (3) releasing hatchery produced larvae and juveniles; (4) protecting genitors in sanctuaries; (5) providing artificial habitats and shelters; (6) introducing lobsters into new environments; (7) protecting genitors by setting a minimum and/or maximum legal size; and (8) protecting berried females.

## Methods of Recruitment Enhancement

### Reducing Fishery-Induced Mortality of Prerecruits

This approach was suggested in presentations by Brown and Caputi (this issue) on *Panulirus cygnus* in Western Australia and by Hunt and Lyons on *Panulirus argus* in Florida. The authors showed by laboratory and field experiments and by tagging that handling of undersized lobsters by fishermen may produce (1) mortalities as high as 15%, (2) displacement of animals away from the fishing grounds, and (3) 4% growth reduction due to appendage regeneration. One author also suggested the possibility of an induction of early maturation by selection or adaptation, which would result in a slowdown in somatic growth. The authors recommend improved handling of undersized lobsters and use of escape gaps on the traps in order to avoid injuries to these lobsters.

Reduction of fishery-induced mortality on juveniles is appealing (Davis 1980, 1981) but the presentations made during this workshop only provided recommendations for conservation measures; they did not report tangible results on enhancement of recruitment after enforcement of such measures. I am unaware of any set of data that would demonstrate that protection of the prerecruits in a lobster fishery had a direct positive effect on subsequent landings and that this effect could be statistically filtered out from natural population fluctuations.

## Collecting and Protecting Young Lobsters from the Wild

Enhancing recruitment by collecting larvae or young stages in the wild and "protecting" them from predation until they reach a stage in which natural mortality is low has been tried with limited success in Japan with penaeid shrimps and in many countries with scallops.

Attempts to attract postlarvae of *Homarus americanus* on collectors floating or hanging in open water or spread on the bottom have been almost totally unsuccessful. Some postlarvae were eventually caught on collectors set close to the bottom or on the bottom, but there is no evidence that these devices acted better than the natural substrate. Homarid and palinurid postlarvae are morphologically very different; the first seem to be adapted to settle on the sea floor and dig burrows, and the latter have appendages differentiated for actively clinging to floating substrates such as seaweed.

Attempts to collect puerulus larvae of spiny lobsters have been successful in Australia, California, Florida, and New Zealand. Collectors mimicking seaweed or floating debris have been used to catch larvae of spiny lobsters mainly for obtaining indices of abundance or recruitment to the grounds and for predicting recruitment to the fishery in subsequent years (Booth 1979; Little and Milano 1980; Phillips 1981; Phillips and Hall 1978). There are contradictory reports, however, that the settlement of pueruli is usually in excess of the maximum carrying capacity (Chittleborough 1979). There is no indication that these experimental results may lead to an efficient way of attracting postlarvae for enhancing recruitment.

Collection of lobster larvae or postlarvae for the special purpose of protecting them from predation and therefore enhancing recruitment has not gone much further than project design (Alvarez 1980). There was no presentation made specifically on this topic during the recruitment enhancement session.

## Releasing Hatchery-Produced Larvae and Juveniles

Enhancing recruitment by production of *Homarus* larvae or juveniles in hatcheries and releasing them on adequate natural substrates has been tried many times. Some of the programs resulted from reorientation of aquaculture experiments when it was realized that rearing lobsters to commercial size was technically feasible, but long and costly. An early release of young individuals on depleted fishing grounds might improve recruitment if there existed a "bottle neck" in natural mortality of young individuals in the wild and if this "bottle neck" could be by passed without having to raise individuals to commercial size. Experiments are ongoing in England, France, Norway, Scotland, and Wales. Presentations on this topic were made by Bannister, Howard et al., and Lorec (papers presented at the workshop). This methodology has not been tried for spiny lobsters due to the difficulty of rearing larvae from the egg through the phyllosoma stages to the puerulus and postlarval stages.

Techniques have been developed for testing the success of the release of masses of young individuals (Poval et al. 1984). The simplest approach consists of following an index of abundance in commercial catch (such as average catch per trap) over a series of years to detect any significant departure from natural fluctuations in recruitment (Le Gall and Jezequel 1977; Le Gall et al. 1983). Another approach consists of releasing "tagged" young individuals and attempting to detect these later on in the commercial catches. The tags may be of genetic nature; a selection of coloured strains (red or blue) has been tried, and a selection of strains bearing a genetical "tag" recognizable by electrophoresis has been suggested (Hedgecock 1977). Release of hybrids of a *H. americanus* and *H. vulgaris* cross has been tried in France. An ongoing technique consists of using "microtags"; minute pieces of magnetized wire are inserted in the flesh of small lobsters, and these can be detected later from the catch by using a magnetometer (Howard, pers. comm.).

Repopulation by massive releases of early larval stages of *Homarus* spp. has either been totally unsuccessful or has not been sufficiently well documented to allow for statistical analysis of detectable effects within time series of catch or catch per unit effort. There are numerous records of larvae being eaten immediately by predators when released at the surface, or swimming up from the substrate when released on the sea bottom by divers.

Repopulation by release of stage IV larvae or young *H. gammarus* up to 2 yr old is being attempted in France around the isle of Houat. So far, it has not produced detectable effects on fishery landings (Lorec paper presented at the workshop). The effects of the experimental releases are very difficult to identify because the natural annual fluctuations in recruitment to the fishery may be as wide as twofold around Houat. A good yearly catch was reported in 1975 but this was observed all along the coast of Brittany (Latrouite, poster presented at the workshop) and could not be attributed to artificial repopulation of the grounds around Houat.

Detection of tagged individuals released as juveniles during stocking and subsequently caught in commercial creel is limited to a few instances. Recapture of $F_1$ hybrids *H. americanus* × *H. gammarus* in France is doubtful. Some "hybrids" were reported captured by fishermen but the morphological characters used for identifying them (number of spines on rostrum and shape) are encountered as a rare variant in natural populations of *H. gammarus*. Electrophoretic analysis of enzymes did not demonstrate clearly that the "recaptures" were actually hybrids (Audouin, IFREMER, Ile d'Yeu, France, pers. comm.). There are no reports of release and recapture of lobsters genetically "tagged" either by colour or by presence of rare enzymatic variants. There is at least one unpublished record of a microtagged lobster released as a juvenile and recaptured at commercial size in Scotland (Bannister, pers. comm.). I am unaware of any such results for spiny lobsters.

## Protecting Genitors in Sanctuaries

Enhancing recruitment by creating sanctuaries in which adult lobsters are protected from fishing has been tried at fishermen's initiatives in almost every fishing country. It was assumed that homarid and/or palinurid lobsters would be allowed to produce larvae which may stock neighbouring fishing grounds. Enhancing production of larvae has been attempted in France by re-

leasing egg-bearing females on the sanctuaries and by selectively harvesting the males. It was assumed that one male may serve several females. Reducing the number of males would lessen competition for food and shelter when maximal carrying capacity of the environment was approached. Most sanctuaries were set up in locations selected intuitively by fishermen rather than after thorough environmental surveys.

Testing the success of the methodology was attempted by using indices of abundance (catch per trap during experimental fishing) on sanctuaries and on the neighbouring fishing grounds. I am unaware of any long-term study documenting a statistically significant impact of sanctuaries on recruitment.

The French experiments reported by Latrouite (presentation at the workshop) provide data bases of experimental fishing on sanctuaries around the coast of Brittany over periods of up to 18 yr. Most of these sanctuaries were set up in the 1950's or 1960's when catch per unit effort of *H. gammarus* declined and stabilized at a level about half that immediately after the Second World War. The catch per unit effort fluctuated considerably from year to year on the sanctuaries. The year 1975 produced a good recruitment on both the sanctuaries and on exploited grounds. The populations of *H. gammarus* on the sanctuaries tended to contain larger, possibly older individuals than on neighbouring exploited grounds. The sex ratio remained well balanced despite removal of males and introduction of berried females on some sanctuaries. The catch per unit effort on sanctuaries was highly variable, possibly due to variability in catchability over time or to variability in abundance. In newly set sanctuaries, an increase in biomass of about twofold over the first 5 yr may frequently be inferred from catch per unit effort. This initial increase is followed by erratic annual variations eventually ranging down to the initial value observed at the start of the experiment. An increase in recruitment observed on fishing grounds neighbouring the sanctuaries has not been demonstrated to differ significantly from similar increases observed simultaneously in remote locations.

I was unable to locate long-term time series of data for sanctuaries of *H. americanus* or spiny lobsters. There was no mention made of successful recruitment enhancement on sanctuaries of these latter species during the workshop.

### Providing Artificial Habitats and Shelters

Enhancing recruitment and growth by providing artificial habitats and shelters has been tried in many countries (Calinski 1981; Hruby 1979; Scarratt 1968, 1973; Sheehy 1976, 1979, 1982): it has been documented in Canada, France, Japan, and the United States. The technique is based on the assumption that shelter is a limiting factor for the abundance of lobsters. Tests must be made to determine whether "artificial reefs" simply concentrate existing populations or actually enhance recruitment by allowing postlarvae to settle and obtain protection and food from the artificial substrate.

Enhancement of recruitment and growth of *P. argus* is reported to be successful in the Gulf of Mexico and is advocated in Florida. A presentation was made by Miller at the workshop. Fishermen have built artificial reefs since the late 1960's. Some authors have claimed that productivity was enhanced through the provision of shelters in the presence of predation on shelter limited sandy bottoms, or that the artificial reefs enriched the area in food organisms, or that artificial reefs allowed settlement of pueruli and postlarvae. In contrast, other authors concluded that the environment was not shelter limited and that artificial reefs simply concentrated adults by reducing "nomadism," therefore acting as a fishing gear. Miller indicated that there is a lack of controlled studies on habitat enhancement.

Information was provided by Scarratt (1968) on an artificial reef in Northumberland Strait (Canada) for *H. americanus*. The colonization of the reef was followed from 1966 to 1973. Initial colonization was by vagrant lobsters and occupation of the site mostly was transitory, possibly due to lack of food. The early colonizers were relatively large and there was no evidence of larval settlement. After 5 yr, lobsters of all sizes were encountered on the reef and the biomass became larger than on natural grounds around the reef (Scarrat 1973). Again in this case it is not possible to differentiate the lobsters which moved onto the reef from neighbouring grounds from those that actually settled and developed on the reef. There is no measure for an increase in productivity or recruitment directly attributable to the reef.

### Introducing Lobsters into New Environments

Recruitment enhancement techniques can also be evaluated from the results of experimental introductions of lobsters into new environments: *H. americanus* and *H. gammarus* in the Pacific (Barber 1983) and *Jasus lalandii* in France. Introduction of adult *H. americanus* from the east to the west coast of North America has been attempted about 30 times. Most of these projects consisted in establishing a small population of mature adults which were expected to mate and produce larvae colonizing the new environment. The attempts so far failed in establishing harvestable populations. However, *Homarus* specimens still are caught occasionally from California to British Columbia. Lobsters recently caught in British Columbia were reported to belong to a second generation after introduction.

Similar attempts were made in Japan using juvenile *H. americanus* with no success. More recent experiments of introduction of *H. americanus* and *H. gammarus* in Japan were reported by Kittaka (paper presented at the workshop). Young *Homarus* of both species are produced in hatcheries and released on artificial biotopes simulating the natural environment in order to enhance their viability after release. These biotopes are built in cages suspended from the sea surface or set on the ocean floor or in large outdoor tanks. The young lobsters survive and grow well without requiring artificial food; they feed on local organisms spontaneously developing in the biotope. The lobsters are reared in groups. The survival is 18–24% after 2 yr at densities of 32–59 individuals/$m^2$. When fourth- to fifth-stage larvae were released experimentally in the natural environment, no recoveries were reported. However, of 80 individuals released at the age of 1 yr, 1 was recaptured 4 yr later at a weight of 1.5 kg. Young *H. americanus* appeared to grow faster and to allow greater carrying capacities than *H. gammarus*. Despite interesting experimental results, no populations of *H. americanus* or *H. gammarus* have been established in Japan.

The introduction of large numbers of adult *J. lalandii* was attempted in France some 15 yr ago. The animals were released in northern Brittany on a rocky coast similar to their natural habitat. The success of this attempt was checked by recaptures from experimental fishing or from commercial fishing. The lobsters crawled over distances as long as 500 km. There are no reports of captures of second-generation animals; however, a curious report was made a few years ago of a few specimens of

*Jasus* caught in the Azores. Being aware of the oceanwide drift of the larvae of *P. cygnus* in western Australia, it is challenging to hypothesize that there might be a link between the French experiment and the Portuguese encounter.

### Protecting Genitors by Setting a Minimum and/or Maximum Legal Size

Protection of immature lobsters by setting a minimum legal size is a technique widely used in North America where it has become a fishery management tool widely accepted by biologists, fishermen, and managers. The justification is usually based on fecundity per recruit calculations, a variation from the dynamic pool family of models integrating growth, mortality, and a fixed relationship between number of eggs and weight of the female. Inevitably, such models lead to the conclusion that allowing more females to survive to adulthood will increase dramatically the production of eggs.

However, density-dependent effects on the relationship modelling the number of hatching eggs versus the weight of the female (generally a simple constant multiplicative factor) are usually not taken into account. It is now known that survival of the eggs in the broods may widely vary between areas due to predation or to parasitism (Brattey et al. 1985), but there is yet no data documenting a density dependence of this survival.

Some authors claim that large females of *H. americanus* will spawn every year although they do not moult, and that enforcing a maximum legal size would therefore considerably enhance egg production. However, in the Gulf of St. Lawrence, the proportion of females bearing eggs in the catch decreases so dramatically as a function of size (poster papers presented at the workshop by Maynard et al. and Moriyasu and Mallet) that it is questionable whether a maximum legal size would be beneficial at all.

The protection of males by a minimum size is usually designed for increasing yield per recruit rather than fecundity of the stock. It is assumed that enough males will always be present to serve the females. For this reason, age at maturity of the males is not well known and may have been misinterpreted (poster paper presented at the workshop by Conan et al.; Conan et al. 1985).

The successful enhancement of egg production and eventually recruitment by setting legal sizes has never been documented experimentally. The assumption that this approach is efficient solely relies on predictions derived from simple-minded models. In countries such as Australia or France, legal sizes are justified by market reasons or yield per recruit enhancement rather than by recruitment enhancement ethics.

### Protecting Berried Females

This approach to recruitment enhancement is widely used and usually strongly requested by fishermen. In France, fishermen have sometimes gone to the point of requesting that female *H. gammarus* bearing eggs be protected by stocking in pens or large reservoirs. Dynamic pool models quite evidently show that the more you protect egg-bearing females from the fishery, the more eggs will be produced. However, as usual, incidence of possible density-dependent mechanisms on natural mortality of the females, on number of eggs spawned, and on survival of the eggs in the brood is unknown and therefore declared negligible. I have been unable to identify well-documented experiments demonstrating enhancement of egg production and recruitment by protection of berried females.

## Recommendations by Participants to the Seminar

The participants to the recruitment enhancement special sessions discussed the feasibility of the various approaches in light of the experience gained. They agreed to issue the following recommendations.

Artificial means for increasing recruitment are at present used experimentally to better understand stock–recruitment relationships and density-dependent mechanisms.

Under special circumstances, and in special areas, repopulation of existing fishing grounds for *H. gammarus* could be promising in the near future. At the present state of our knowledge, it is felt that this technique should be used mostly as an experimental tool.

Artificial reefs should be used as an experimental tool for a better understanding of the basic components of stock recruitment, density dependence, production, and maximum carrying capacity. It is not felt that artificial reefs may be an adequate way of enhancing production unless shelter is a limiting factor in areas such as sandy bottoms and eel or turtle grass bottoms, particularly for palinurids and in special cases for homarids.

Situations in which egg production is the limiting factor are likely to be scarce. Sanctuaries are unlikely to contribute substancially to recruitment unless the areas are very large and adequately situated upstream from larval drifts to commercial fishing grounds. It is felt that sanctuaries may not be an efficient way of enhancing in situ production. Sanctuaries may be an efficient research tool for studying density-dependent effects.

Maintaining berried females in pens as a means of increasing larval production is not considered efficient. In situations where egg production may be a limiting factor for recruitment, when stock density has been reduced considerably, traditional methods such as increasing size at first capture of females above maturity size would appear to be more efficient than artificial reefs, sanctuaries, or pens for berried females.

Reducing fishery-induced mortality of juveniles by using escape gaps or avoiding their capture as by catch in other fisheries could be an efficient and low-cost method for enhancing recruitment.

## Discussion and Conclusions by the Author

References on recruitment enhancement of lobsters are extremely scarce. Most of the information comes from unpublished manuscripts and reports. An automatic literature search in *Aquatic Sciences and Fisheries Abstracts* provided only 10 references, most of them dealing with short-term experimental results or initial setup of projects. No successful experiments on a population scale were reported.

From the literature reviewed and from the presentations made at the seminar, it appears that although many years have elapsed since some recruitment enhancement experiments were initiated, a subsequent scientific followup provided time series of observations in only a few cases. Recent experiments are controlled more rigorously but the data are not fully available.

None of the initiatives of stocking or restocking of larvae or adult lobsters reviewed during the workshop have proven to be successful for restoring the optimal potential of a known fishery

or developing a new harvestable stock, but the past experiments were seldom rigorously planned and controlled. Creation of artificial reefs or sanctuaries for enhancing recruitment also remains of uncertain utility. It is difficult to discern, even over long time series, any benefit of artificial recruitment enhancement from natural population fluctuations. The sanctuaries and artificial reef experiments show that the virgin biomass of an unexploited stock may be about twice as high as that of an exploited one. This conforms to the theory of surplus production models predicting a maximum sustainable yield at one third to one half of the initial biomass. This would indicate that there is not much to gain by creating sanctuaries for increasing growth or recruitment. The rate of surplus production would be decreased as biomass increased.

No recruitment enhancement method has so far been demonstrated to be efficient in the natural environment even on an experimental scale. This in no way means that well-designed experimental setups for studying repopulation are lost causes. It is important to bear in mind that none of the more widely accepted remedies such as protecting berried females or setting a minimal legal size above age of first reproduction have been shown to be efficient measures, either by rigorous experimental approach or by analysis of long-term series of data. Fishery biologists and fishermen actually have behaved similarly.

The former have advocated management measures based on hypothetical stock–recruitment models which have never been supported by facts. The latter have demanded management measures such as protection of berried females or release of larvae for restocking the grounds which are based on simple "logical" deductions. Both approaches are the expression of an anthropomorphic intuitive interpretation of nature and not of rational analysis.

A logical approach is required for analyzing recruitment mechanisms before mathematical modelling and prediction may become efficient. The effects of physical environment factors such as residual currents and gyres on the larval drift and larval retention must be understood. The density-dependent processes in the life history and behaviour of larvae, postlarvae, and juveniles must be identified. An experimental approach in natural or simulated habitats should be used for analyzing density dependence of growth and mortality. Well-designed experiments on stocking or restocking of grounds may provide such information in the near future although present results remain limited and sketchy.

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## References

ALVAREZ, T. S. 1980. Consideraciones preliminares de un proyecto de semicultivo de langosta roja *Panulirus interruptus*. Memorias del 2. Simposio Latinamericano de Acuacultura 1: 2099–2112.

BARBER, F. G. 1983. Lobster transplant to Masset Inlet. Can. Tech. Rep. Fish. Aquat. Sci. 1181: 10 p.

BOOTH, J. D. 1979. Settlement of the rock lobster, *Jasus edwardsii* (Decapoda:Palinuridae), at Castlepoint, New Zealand. N.Z. J. Mar. Freshwater Res. 13(3): 395–406.

BRATTEY, J., A. CAMPBELL, A. E. BAGNALL, AND L. S. UHAZY. 1985. Geographic distribution and seasonal occurrence of the nemertean *Pseudocarcinomertes homari* on the American lobster, *Homarus americanus*. Can. J. Fish. Aquat. Sci. 42: 360–367.

CALINSKI, M. 1981. Artificial reefs as strategic nursery ground, p. 209–210. *In* D. Y. Aska [ed.] Rep. Fla. Sea Grant Program. Artificial reefs: Proceedings of a conference held Sept. 13–15, 1979, Daytona Beach, FL.

CHITTLEBOROUGH, R. G. 1979. Natural regulation of the population of *Panulirus longipes cygnus* George and response to fishing pressure. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 1975: 217–221.

CONAN, G. Y., M. COMEAU, AND M. MORIYASU. 1985. Functional maturity of the American lobster *Homarus americanus*. Int. Counc. Explor. Sea ICES C.M./K:29: 56 p.

DAVIS, G. E. 1980. Juvenile spiny lobster management or how to make the most of what you get. Fisheries 5(4): 57–59.

1981. Effects of injuries on spiny lobster, *Panulirus argus*, and implications for fishery management. Fish. Bull. 78(4): 979–984.

HEDGECOCK, D. 1977. Biochemical genetic markets for broodstock identification in aquaculture, p. 523–531. *In* Eighth Annu. Meet. World Maricul. Soc., San Jose (Costa Rica), 9 Jan. 1977. Louisiana State University, Division of Continuing Education, Baton Rouge, LA.

HOWARD, A. E., AND D. B. BENNETT. 1979. The substrate preference and burrowing behaviour of juvenile lobsters (*Homarus gammarus* (L.)) J. Nat. Hist. 13(4): 433–438.

HRUBY, T. 1979. Experimental lobster ranching in Massachussetts, p. 194–202. *In* J. W. Avault [ed.] Proc. Tenth Annu. Meet. World Maricult. Soc., Honolulu, HI. Louisiana State University, Division of Continuing Education, Baton Rouge, LA.

LE GALL, J. Y., AND M. JEZEQUEL. 1977. Variabilité annuelle du recrutement dans une pêcherie littorale de homard, *Homarus gammarus* en Bretagne. Cons. Int. Explor Mer CIEM C.M./K:14: 21 p.

LE GALL, J. Y., M. JEZEQUEL, J. LOREC, AND Y. HENOCQUE. 1983. Evaluation de la variabilité annuelle de recrutement d'une pêcherie littorale de homard (*Homarus gammarus*) en Bretagne (Ile d'Houat) 1973–1980. La Mer 21(2): 102–112.

LITTLE, E. J. JR., AND G. R. MILANO. 1980. Techniques to monitor recruitment of postlarval spiny lobsters, *Panulirus argus*, to the Florida Keys. Fla. Mar. Res. Publ. Rep. 18 p.

PHILLIPS, B. F. 1981. The circulation of the southeastern Indian Ocean and the planktonic life of the western rock lobster. Oceanogr. Mar. Biol. Annu. Rev. 19: 11–39.

PHILLIPS, B. F., AND N. G. HALL. 1978. Catches of puerulus larvae on collectors as a measure of natural settlement of the western rock lobster *Panulirus cygnus* George. Rep. Div. Fish. Oceanogr. CSIRO Cronulla 98: 18 p.

POVAL, P. J., W. COOK, AND P. OXFORD. 1984. Lobster stock enhancement. Lancashire and Western Sea Fisheries Joint Committee Manuscr. Rep. 8 p.

SCARRATT, D. J. 1968. An artificial reef for lobsters (*Homarus americanus*). J. Fish. Res. Board Can. 25: 2683–2690.

1973. Lobster populations on a man made rocky reef. Int. Counc. Explor. Sea ICES Shellfish and Benthos Comm. C.M./K: 3 p.

SHEEHY, D. J. 1976. Utilization of artificial shelters by the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 33: 1615–1622.

1979. Fisheries development: Japan. Water Spectrum 12(1): 1–9.

1982. The use of designed and prefabricated artificial reefs in the United States. Mar. Fish. Rev. 44(6–7): 4–15.

# Summary of Session 6: Ecology of Population Structure

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Factors affecting recruitment to the fishable stock include changes in the physical environment, food supply, predation, and competition. The term "population structure" was broadly interpreted in this session to include density, size structure, growth, and mortality. An equally wide range of factors affecting these was considered: substrate type, food type and availability, competition, burrowing behavior, and activity patterns. Session participants reported on observations and experiments done on spiny and clawed lobsters that ranged from immediate postsettling juveniles to adults. Despite the variety, general trends emerge and directions for further research are apparent. In this summary, I review the major points made by each contributor and then try to draw some general implications.

## Substrate Effects

The size and availability of crevices or shelters appear to have a marked effect on the population size structure of *Homarus gammarus* (Howard et al., paper presented at the workshop). Substrates with only small crevices will not support a population of large lobsters. Size–frequency comparisons from several areas showed mean size differences that were associated with topography. Further observations in flumes suggest that lobster movement is restricted by high current speeds, suggesting that tidal activity cycles may be keyed to periods of lower flow rates around slack water.

In *Nephrops norvegicus*, population distribution, density, and size structure are at least partially determined by sediment type. *Nephrops* burrow in areas of cohesive muds. Chapman et al. (paper presented at the workshop) showed that mean size of individuals was positively correlated with silt–clay content. The newly settled juveniles of *Nephrops* seek out burrows of the adults to take up residency; they do not make new burrows. In a burrow-limited situation there may be density-dependent mortality of the postsettling stage and recruitment may be limited by both the availability of adult burrows and interaction with the adults.

Growth and mortality of young-of-the-year *Homarus americanus* were measured on several different substrates in small laboratory aquaria by Barshaw and Bryant (paper presented at the workshop). They saw no differences between substrates over the 8-mo period of the study, but implicated eelgrass beds from their behavioral observations to be a good place to look for newly settled lobsters.

## Food and Population Density

Growth of *N. norvegicus* appears to be density dependent and may be limited by food supply (Chapman et al.), since highest growth rates were found in low-density populations on sediments with a high organic content where prey was more plentiful. It seems paradoxical that the highest densities and biomass occur in areas with low organic carbon content that do not offer good conditions for growth, but it was suggested that since recruitment may be limited by the availability of burrows, it may be burrow density rather than food availability that limits population density.

The availability of food to lobsters was the subject of papers presented by Michaud and Elner and Campbell. An exhaustive study contrasting prey type and abundance in kelp forests and in sea-urchin-maintained barren grounds on the east coast of Canada gave the surprising result that there was more invertebrate biomass on the barrens than in the kelp forests. However, Michaud showed that production was about the same in the two areas, and that production of prey preferred by *H. americanus* was higher in the kelp forests than on the barren grounds. Nevertheless, according to Elner and Campbell, the stomachs of lobsters taken from the barren grounds were equally as full as those taken from kelp forests. There was no difference in most prey selected in the two areas. The question must be raised, then, as to just what effect these urchin-denuded areas have on lobster populations.

A possible new food source for newly settled lobsters was reported by Barshaw and Bryant, who made laboratory observations on benthic fourth- and fifth-stage *H. americanus* in U-shaped burrows. The lobsters create a water current by pleopod fanning and apparently take plankton from the water drawn through the burrow. They went on to show that they could survive as well on live zooplankton as on the usual laboratory diet of brine shrimp.

Attempts at understanding the relationship between food availability and population density can only go so far with correlative and observational studies. Experimental manipulations in the field are needed. The only one reported in this session was by Ford et al., who attempted a comprehensive field experiment in which the population density of juvenile spiny lobsters, *Panulirus cygnus*, was lowered by intensive trapping. Growth and mortality rates of the lobsters in the experimental area were compared with those in a nearby control population. A significant decrease in mortality appeared to result from the treatment, but no difference in growth rate was seen. They pointed out that the usual cautions concerning assumptions when determining mortality rates apply here, in particular with regard to density-dependent emigration which might have been a factor. This experiment, although preliminary in nature, points out some of the approaches and some of the problems to be faced if we are to make further progress in understanding food availability and density-dependent effects on lobster populations.

## Competition and Predation

*Homarus americanus* appears to compete for shelter with the

Jonah crab, *Cancer borealis*. Richards and Cobb (this issue) examined the behavior involved on this interaction showing, contrary to expectation, that within the range of sizes examined, size differentials among crabs did not seem to affect the outcome of competition. Equally unexpectedly, the mortality of lobsters increased markedly under competitive stress, while that of Jonah crabs did not. Lawton (paper presented at the workshop) made controlled laboratory observations on time budgeting by small juvenile *H. americanus*. Small lobsters effectively spend all the time in shelter. As size increased from 20 mm CL, so did activity outside shelter. Increasing the period of preexperimental starvation led to more activity during the daylight hours. And, if another lobster was included in the experiment (intraspecific competition), activity level increased but foraging time decreased. It seems that as animals got older or hungrier, they were more willing to take the risks associated with being out of shelter.

## Implications

Some perspectives on Session 6 are in order. First, a comparison with the lobster workshop held 9 yr ago in Perth, Australia, shows that research on ecology and population structure has advanced from a descriptive to a more experimental mode; 1 of 11 abstracts on this topic from that meeting (Phillips and Cobb 1977) was experimental, while 4 of 7 were at this meeting. Second, not only is it becoming clear that density-dependent mechanisms are important in the control of population size, but effort is being directed towards the understanding of these mechanisms. I expect this change in both the perception of the problem and mode of analysis will lead to a rapid accumulation of insights important to the understanding of recruitment processes.

It has long been obvious that substrate type is a prime factor in determining the geographic distribution of lobsters. Now, to "distribution" we must add "and population size structure." Perhaps we should prepare more finely detailed charts of our areas in which we do not simply identify "good lobster ground" and "bad lobster ground" but "good ground for small lobsters," etc. Knowledge of topography can lead to the ability to put limits on the upper bound of the size structure of a population. Within the definition of topography, we clearly must include water current speed and its interaction with bottom type. In Session 8, Caddy (this issue) suggested the application of the concept of the Fractal Dimension for identifying topographic "bottlenecks" in recruitment processes; this would seem a promising approach.

Investigations on density-dependent mechanisms of lobster population regulation are just beginning. It is not yet clear how food supply interacts with rates of growth and mortality, but the work reported by several participants indicate its importance and that we should continue our efforts. In *N. norvegicus*, there may be compensatory mortality during the larval settling period. This exciting speculation should be examined empirically, using all the technology available from behavioral observations to modelling. Interactions with conspecifics and with crabs also have potential for increasing mortality rates both by direct predation during loss of shelter or foraging and by indirect means such as shift to poorer shelter or to less nutritional food.

Much of the work reported in this session focussed on post-settled prerecruits. The behavior and ecology of this stage is little known in any of the lobsters because of their cryptic nature and limited activity outside of shelter. It is clear that more experimental field work, alongside controlled laboratory research, is needed to better understand the ecology of population structure in lobsters.

## References

PHILLIPS, B. F., AND J. S. COBB. 1977. Workshop on lobster and rock lobster ecology and physiology. Circ. CSIRO Div. Fish. Oceanogr. (Aust.) No. 7.

# Summary of Session 7: Factors Affecting Growth and Reproduction

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All factors that influence the recruitment of a lobster are attributable to either heredity or environment. Most of the information presented in this workshop related to the environment. Not surprisingly, temperature proved to be the most pervasive and influential parameter, at least for homarid lobsters. Temperature affects survival, growth, and reproduction, directly or indirectly controlling the rate of embryonic, larval, postlarval, and juvenile development, size at maturity, maturation of the ovary, and successful integration and synchronization of molting and oviposition.

However, information brought out during the presentations and ensuing discussion made it clear that many things other than temperature impinge on the developing organism and modify the dominant influence of temperature, and these interactions produce results that usually defy prediction with current knowledge. For example, the effects of food quantity and quality on larval development under standardized conditions can be easily determined, but results change with variations in the intensity, duration, and wavelength of illumination, with season of the year, with developmental stage, temperature history during embryonic development, and so on. The extent and complexity of these interactions was one of the more revealing aspects of the workshop.

Stress was shown to be a significant factor in survival, growth, reproduction, and eventual recruitment of lobsters, and information on endocrine interactions suggested pathways for expression of such effects. It was reported, for example, that stress can suspend release of the ecdysteroids that are necessary for molt initiation. Thus we have a possible explanation for such puzzling phenomena as the delay of ecdysis by subordinate juvenile lobsters in the presence of a dominant, and the ability of "females-in-waiting" to delay ecdysis until a preferred male becomes available for mating.

Fishing stress was also identified as important in oocyte, embryo, and juvenile–adult mortality. The stress of trap confinement during the late stages of ovarian maturation can cause oocyte resorption and loss of reproductive potential. The greatest impact would therefore fall on those areas with the most intense fishery, i.e. some of our most productive lobster grounds. Discard of sublegal lobsters is another form of fishing stress, the impact of which would increase in proportion to the number of sublegal lobsters on the grounds and the frequency of capture and release.

Some of the interactions between environment and bioenergetics were delineated, and a clear parallel was drawn between nutritional state and survival to recruitment. The role of disease and parasitology in survival and recruitment was also put in perspective by a report on the impact of a nemertean on Dungeness crab populations on the West Coast. *Homarus*, of course, has its own egg predator, a nemertean not unlike the one that afflicts the Dungeness crab.

As the information accumulated, the usual patterns of old, new, and conflicting results emerged. The notion that homarid lobsters from warmwater areas (Gulf of St. Lawrence, Western Long Island Sound) grow faster than those from colder oceanic exposures was challenged and should therefore be reexamined. Also challenged was the notion that larvae and postlarvae from females in cold-water areas are larger than those from females in warmwater areas. Recent studies show no consistent relationship between temperature of origin and resulting larval size.

Other old concepts were confirmed. The occurrence of intermediate larval stages and the responses of larval *Homarus* to temperature were found to be exactly as Templeman described them nearly 50 yr ago.

But there were also some new concepts. Evidence was presented that advancing age is not accompanied by declining reproductive potential. Spiny lobster biologists disagreed on this point, but the consensus of those working with *Homarus* was that reproductive senility is not a problem. On the contrary, consecutive spawning, multiple fertilization (two or more spawnings from a single mating), and intermolt mating (all of which occur in spiny lobsters as well) allow very large female American lobsters to actually spawn more frequently than smaller ones in which spawning and molting occur in alternate years. In addition, the logarithmic relationship of fecundity and length in American lobsters may mean that the "global" relative fecundity of very large lobsters is much greater than previously supposed.

Hopefully, this new concept will bring about a reappraisal of existing models and management strategies. If large females represent a portion of the "refugium" concept so eloquently developed by Anthony and Caddy (1980) in the proceedings of the 1978 Canada–U.S. Workshop, their depletion could have serious implications for the entire fishery.

Which brings me to the final factor that can affect growth, reproduction, and eventual recruitment: *fisheries management*. Good management should lead to enhanced recruitment. Since biological information forms the theoretical base for sound management, good biological information should lead to good (or at least better) management. This point is often overlooked in the rush to develop models and accumulate numbers. The "garbage-in, garbage-out" axiom is a fact of life. Models derive their validity from the biological facts on which they run. Fisheries managers would be well advised to insist on the best biological information that research can produce.

## References

ANTHONY, V. C., AND J. F. CADDY [ED.]. 1980. Proceedings of the Canada–U.S. Workshop on status of assessment science for N.W. Atlantic lobster (*Homarus americanus*) stocks (St. Andrews, N.B., Oct. 24–26, 1978). Can. Tech. Rep. Fish. Aquat. Sci. 932: 186 p.

# Summary of Session 8: Models of Stock–Recruitment Relationships

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Mathematical models have played a central, if controversial, role in the ecological sciences. Recent critiques of modelling in both the ecological and fisheries literature have drawn attention to problems in existing approaches and practices (see Francis 1980; Pielou 1981; Simberloff 1981; Hall and DeAngelis 1985). The proliferation of alternative models and, in some cases, the lack of attention to validation of model assumptions and structure have fueled the debate on the utility of modelling. The current controversy is a healthy exchange which should serve both to clarify the proper role of modelling in ecological research and to strengthen the linkage between field and analytical studies. Despite the potential problems, I feel that it is inarguable that the types of questions raised in population studies in general, and fisheries science in particular, require quantitative solutions. For example, we are required to predict the ways in which populations are changing over time, the fraction of the population that can be harvested without affecting reproductive potential, or the expected yield under alternative exploitation regimes. Often the answers to these questions are characterized by uncertainty; nevertheless, we require a formal set of rules which describe the interrelationships among the components of the system (i.e. a conceptual model). The interplay between biological investigation and modelling is critical. Modelling may be irrelevant without specific reference to real systems and without the feedback generated by validating model prediction against observation. In turn, a model may provide a structural framework which serves to identify critical variables or interactions, thus guiding research priorities.

Modelling may serve many functions ranging from the extraction of general principles to the development of quantitative predictions. In many fishery-related studies, it is necessary to specify a realistic model structure. To a large degree, the accountability of the fishery scientist for specific management recommendations requires an emphasis on realistic model formulation. This argues for a strong linkage between empirical and analytical studies in fisheries research. The roles of the analyst and biologist should be complementary (or indeed combined). In this context, modelling of fishery systems is not an esoteric exercise but rather an indispensable component of the process of providing management advice.

Has modelling played its proper role in the context of this workshop? I would like to address this question with specific reference to traditional stock–recruitment models. The classical stock–recruitment models of Ricker (1954) and Beverton and Holt (1957) are derived from simple differential equations describing the decay of a cohort over time with stock-dependent and density-dependent mortality, respectively (see Harris 1975 for a review). The theoretical basis for the models may therefore be expressed in terms of elementary demographic principles. Since the cohort must decline with time, the basic structure of the underlying differential equation is known. It remains only to determine if some form of compensatory mortality exists. The question may be addressed in two ways. First, we may collect a time series of population size estimates at the various life history stages and see if the data conform to the predicted form under density-dependent or stock-dependent mortality. In essence, we are trying to deduce the dynamics of the system by its output — in this case, the abundance at successive life history stages. Often, due to a combination of measurement error and random variation in survival, this approach will not be entirely adequate, since it may be difficult to discern the form of the relationship between stock and recruitment. A series of questions may then be posed which would allow us to differentiate among competing hypotheses for the existence and nature of compensatory control. I would suggest that these may be posed in a way which is amenable to experimental or observational verification. Since competing hypotheses about the nature of compensatory control require distinctly different biological mechanisms, we can design studies to test these mechanisms from first principles. To illustrate this point, it is known that an overcompensatory or Ricker-type response can only be generated by quite specific mechanisms: for example, cannibalism by the parents, delayed passage time through a predatory field due to density-dependent growth, or depletion of critical resources by the stock. In contrast, mechanisms generating a Beverton–Holt recruitment function include competition for food or space among members of the cohort. Approaches to addressing the importance of these factors in the field, and possibly in the laboratory, are clear although not trivial in an operational sense. An excellent example is afforded by studies of Dungeness crab populations off northern California described by Botsford (this issue) at the workshop. Cyclical patterns in annual landings indicated the possibility of an overcompensatory recruitment mechanism. Since cannibalism may generate a response of this type, field studies were undertaken to ascertain whether cannibalism occurs in natural populations. Alternative mechanisms such as environmental forcing factors are also being investigated. Thus, in the first case, a specific population mechanism was hypothesized based on patterns in abundance levels and a program has been implemented to systematically test causal factors. The point is that these questions may be addressed at several levels and that the models are sufficiently explicit in their assumptions and derivations to direct biological studies to help resolve ambiguities in the empirical data. Progress will be most rapid with a sequence of sound empirical observation and model formulation and validation. Specific biological studies may then be used to test possible mechanisms.

Models of the dynamics of exploited populations are simplified representations of real systems. Careful observation of natural populations provides the key to indicating where greater complexity in model formulation may be required to realistically reflect the natural system. For example, in their sim-

plest (and most common) form, stock–recruitment models assume that the parameters are time invariant. Momot (paper presented at the workshop), working on crayfish production in freshwater systems, has documented trends in critical environmental factors (notably changes in available nursery habitat in the littoral zone) in certain lakes. Survival rates of juvenile crayfish are directly affected. A more complex recruitment model which explicitly accounted for temporal changes in environmental factors would be required to model crayfish recruitment dynamics. To provide a different type of example, studies described by Mohn and Campbell (paper presented at the workshop) indicate the potential importance of incorporating spatial heterogeneity in population dynamic models. Most fishery production and recruitment models ignore spatial dynamics. Detailed studies of migratory patterns and larval dispersal in large-scale hydrographic systems are required to resolve the appropriate spatial scales for modelling recruitment dynamics.

A common theme in each of the papers in Session 8 was the relative importance of compensatory population controls in lobster, crab, and crayfish stocks. It was further recognized that crustacean species are characterized by a complex life history pattern comprising a number of distinct stages at which compensatory control is possible. Caddy (this issue) argued that the expected form of the stock–recruitment function is asymptotic, possibly related to competition for settlement space. Caddy further developed the concept of "niche space" limitations, using the theory of fractal surfaces. Essentially, it was argued that the number of potential niche spaces (shelter sites) varies for different sized individuals. Due to the higher number of small individuals, however, shelter limitation is greatest for the smaller size categories. From a somewhat different perspective, Mohn and Campbell examined the consequences of shelter resource limitation and found that the consequences differ depending on the period(s) during which shelter limitation may occur. An asymptotic function was obtained when this limitation occurred during the first year of life, while a dome-shaped function was obtained when shelter limitation occurred at all ages. Based on empirical evidence, Fogarty and Idoine (this issue) argued that the settlement stage of *Homarus americanus* may be a critical period when density-dependent effects, particularly competition for shelter, may be particularly evident. No evidence of compensatory control was evident during the pelagic larval phase. Bannister and Addison (this issue) described models which considered the implications of alternative shapes of the stock–recruitment function and which also considered shelter limitation for larger-sized individuals, resulting in increased mortality in the larger size-classes.

A second major theme in the session was the potential importance of environmental effects on recruitment. Caddy reviewed environmental factors which have been related to lobster recruitment or some index of recruitment including temperature, river discharge, and other variables and noted the importance of chance environmental factors in recruitment variability. Botsford examined the possibility that a nonlinear wind effect could be responsible for the cycles in Dungeness crabs, possibly when acting in concert with density-dependent mechanisms. For crayfish, Momot described temperature influences on time required for juveniles to pass through a predatory field. In addition, change in habitat quality was noted for one lake. Large-scale changes in environmental conditions may have a direct effect on recruitment and obscure any underlying stock–recruitment relationship. One approach is to try to partition variability in recruitment into stock-related and environmentally related sources. For example, a stock–recruitment relationship may be fit and the residuals from the stock–recruitment model regressed against one or more environmental variables. An alternative approach is to develop a stock–recruitment model with direct environmental parameters or to develop stochastic models, which explicitly consider the importance of random variability in recruitment processes.

A third major issue addressed at the session was the coupling of yield-per-recruit and stock–recruitment models. Bannister and Addison noted that models which directly incorporate stock–recruitment relationships often lead to more conservative results than consideration of yield-per-recruit curves alone. Exact results depend on the form of the stock–recruitment curve. If a depensatory stock–recruitment curve obtains, the possibility of a stock collapse is increased. Caddy provided several examples where crustacean life histories could lead to depensation. An important point is that under certain circumstances (e.g. the case described by Addison (this issue) where natural mortality increases with size), there may be little or no warning of an impending collapse based on changes in CPUE or in size composition. Caddy had earlier noted the importance of stock–recruitment considerations for fisheries characterized by high levels of fishing mortality and that yield-per-recruit alone is insufficient. Caddy further observed that high "unit" value of most crustacean species and the tendency for price to be elastic (i.e. continually increase as abundance or CPUE decreases) lead to overexploitation and the possibility of a stock collapse. The age-structured models used in analysis of the Dungeness crab fishery directly incorporate stock–recruitment considerations and are therefore consistent with the general approach described by Bannister and Addison, although in a different framework.

Of the common themes which emerged from the session, perhaps the most striking was the indication of the importance of events in the early life history stages of many crustacean species and the general lack of detailed information on the behavior and ecology of these stages. Further research efforts should be directed at the postsettlement stages; both field and laboratory studies would be required to examine important factors, such as the relative importance of cannibalism, factors affecting habitat selection, and intraspecific shelter competition and its implications for vulnerability to predators. It is probable that long-term monitoring programs alone will not be sufficient to resolve questions on the mechanisms regulating crustacean populations. The most fruitful approach would appear to be a combination of long-term field studies and investigations designed to test hypotheses regarding specific mechanisms.

## References


BEVERTON, R. J., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. Fish. Invest. Lond. Ser. 2: 19.

FRANCIS, R. C. 1980. Fisheries science now and in the future: a personal view. N.Z. J. Mar. Freshwater Res. 14: 95–100.

HALL, C. A. S., AND D. L. DEANGELIS. 1985. Models in ecology: paradigms found or paradigms lost? Bull. Ecol. Soc. 66: 339–346.

HARRIS, J. G. K. 1975. The effect of density-dependent mortality on the shape of the stock and recruitment curve. J. Cons. Explor. Mer 36: 144–149.

PIELOU, E. C. 1981. The usefulness of ecological models: a stock-taking. Q. Rev. Biol. 56: 17–31.

RICKER, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11: 559–623.

SIMBERLOFF, D. 1981. The sick science of ecology. Eidema 1(1).

# Summary of Session 9: Summary of Research Recommendations

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The papers presented at the International Workshop on Lobster Recruitment held at St. Andrews during 1–5 July, 1985, indicated that much progress in understanding lobster biology and recruitment has been made since the previous Workshop on lobster ecology and physiology held in 1977 in Perth, Western Australia (Phillips and Cobb 1977). The ability to forecast yields has progressed for the Western Australia rock lobster fishery, using larval settlement and juvenile abundance indices (Caputi and Brown, this issue; Phillips, this issue). However, for most other lobster fisheries, recruitment prediction capability has not developed, although considerable information relevant to the problem has emerged. The basis for population regulation and for recruitment variability which occurs in the early lobster life stages remains uncertain, and this lack of understanding hinders improvement in the management of many lobster fisheries. The purpose of this paper is to provide a summary for research direction, as recommended by the Workshop participants, that will permit a better understanding of population regulation and recruitment in lobster fisheries.

## Lobster Fisheries and Recruitment Variability

### Stock Identity

Identifying "unit stocks" and genetically distinct populations remains a problem with many lobster fisheries. The Workshop suggested that efforts should be coordinated to define appropriate techniques (e.g. mitochondrial DNA, biochemical genetic markers, electrophoresis, etc.) to assess larval origins and for "tracking" larval distribution and movements.

Evidence to postulate the existence of reproductive units (cells) for both homarids and palinurids is varied. Contranatant movements of juveniles and adults to spawning grounds has been shown for several palinurid stocks (e.g. Herrnkind 1980; Moore and MacFarlane 1984; Booth, this issue). Whether this type of process occurs in homarids is less clear, although seasonal depth migrations have been established (Cooper and Uzmann 1980; Campbell, this issue). This emphasizes the need for detailed spawner–recruitment studies on discrete stock units such as those of the Magdalene Island (*Homarus*), Hawaii and Bermuda (palinurids), and the Irish Sea (*Nephrops*).

### Forecasting and Management

At present, many lobster fisheries are managed mainly using size, effort, and berried female regulations. Accurate yield forecast would be useful to assist lobster fisheries management to prevent overfishing and to utilize a quota system to assist fishermen in forecasting monetary and manpower requirements (e.g. purchase of new equipment) and to consider alternative species fisheries. Although the recruitment processes and causes of fluctuations in year-class strength may not be fully understood, larval and juvenile abundance indices are used to forecast yields for the management of the Western Australia rock lobster fishery (Caputi and Brown, this issue; Phillips, this issue). It would seem desirable to develop similar forecasting systems for other palinurid and homarid fisheries.

## Larval Distribution Dynamics

The life history of most lobster species is characterized by relatively long-lived individuals, the females of which have many broods and high fecundity and pelagic larval stages that swim in oceanic currents and some that settle in appropriate juvenile habitats. Recent results lead to clearer understanding of (1) oceanic current patterns, (2) vertical migration of lobster larvae in the water column (M. Farmer et al., pers. comm.; Phillips and McWilliam, this issue; Hudon et al., this issue; G. Harding et al., pers. comm.), and (3) that individuals of the last larval stage of some lobsters are active swimmers and may have the capability of selecting habitats for settlement (Phillips and McWilliam, this issue; Ennis, this issue; J. S. Cobb, pers. comm.). However, the debate between the enthusiasts for directed larval migration versus stochastic dispersal processes (e.g. Ennis, this issue) probably will continue.

For most lobster species, there is no clear understanding of the swimming abilities of larvae in relation to chemical and physical cues. Laboratory and field experiments are required to understand larval behavior and swimming ability in relation to environmental cues (e.g. light, temperature, pressure, and salinity) and to horizontal and vertical water movements at different spatial scales (e.g. $<10$ m to $>10$ km). We also need to understand how these hydrodynamic mechanisms cause larval mortality. The physical transport of larvae out of a spawning area into unfavorable areas could be a source of mortality due to low food availability and consequent starvation, reducing growth and activity and increasing predation.

There is a need for coordination between biologists and oceanographers to identify currents and gyres that play a role in the recruitment process and to evaluate physical constraints to which larval dispersion, transport, and settlement are subjected. The Session 3 summary by Phillips (this issue) gives recommendations for further research on lobster larvae.

## Behavior and Movement

### Larval Settlement

The transition from the pelagic to the benthic stage may be a critical period or "bottleneck" of survival for many crustacean species. For lobsters, larval settlement behavior is not well understood. There is a need to understand what environmental, chemical, and/or physical cues are used by larvae to settle. The development of a larval settlement collector and its use in predicting recruitment of *Panulirus cygnus* in Western Australia (Phillips, this issue) has prompted the desire to develop collectors for larvae of other lobster species. The Workshop recognized the need to develop field monitoring methods to locate larval settlement habitats. Also, the use of seminatural conditions (e.g. large aquaria) might be useful to infer lobster–habitat relationships.

### Movement

Studies on movement patterns of juvenile lobsters should be encouraged because the extent of their movements is not as well known as those for the adult stages. The Workshop suggested that the following approaches and/or techniques be used in juvenile and adult movement studies: (1) determine the linkages between environmental stimuli and neurohormonal processes that act to regulate lobster movement and migratory behavior; (2) develop automatic ultrasonic tracking equipment effective for recording movement and environmental conditions.

## Recruitment Enhancement

Evaluation of the success of recruitment enhancement techniques should take into account the potential reproductive impact of the introduced animals. Also, the operating costs of rearing and stocking the juveniles should not exceed the catch value of the recruited animals. The evaluation process would require a well-planned experiment with proper controls to provide a degree of proof of recruitment enhancement success, cost effectiveness, and feasibility.

## Ecology of Population Structure

The Workshop identified prerecruit juvenile population dynamics and ecology as an important area for further research. Behavioral factors such as (1) feeding patterns, (2) interactions with predators, and (3) cryptic activity may influence juvenile lobster population dynamics. Substrate type could affect the size composition, food availability, growth, mortality, and distribution of lobster populations in different areas. These factors may or may not limit the carrying capacity of an area. Density-dependent or crevice-dependent mortality and growth effects require further investigation under experimental field conditions. The fractal concept (Caddy, this issue) provides a useful "field theory" for looking at niche size spectra, particularly in relation to identifying bottlenecks in the recruitment process.

Studying aspects of lobster ecology may require that experimental areas be closed to avoid disturbance from fishery activities. Closed experimental areas would allow factors such as recruitment, growth, reproduction, survival, and behavioral processes to be studied on a long-term basis. Examining aspects of social behavior, foraging, and time budgets under field and seminatural conditions also could be useful in understanding intra- and inter-specific interactions between lobsters and associated biota (Atema, this issue; P. Lawton, pers. comm.).

## Factors Affecting Growth and Reproduction

The technology for aging lobsters is still in its infancy and studies are still needed to determine growth rates with age, size at age, and age at maturity for lobster species that have a wide geographic distribution and therefore are exposed to different environmental conditions.

Although advances in understanding lobster ovarian-molt cycles have been made (Aiken and Waddy 1980), the frequency of multiple extrusions and consecutive year spawnings discovered in long-term laboratory observations in large *H. americanus* (Waddy and Aiken, this issue) need to be determined for different field locations and environmental conditions. Where the various physiological events in ovarian-molt cycles under field conditions are known for lobster species, they should be incorporated into the framework of mathematical models used for predicting yield and eggs per recruit and stock–recruitment relationships (Caddy, this issue).

The selection pressures imposed by intensive exploitation by crustacean fisheries with strictly enforced size limits require examination. There may be genetic selection effects by fishing on size at maturity, reproduction, growth rates, and trap avoidance. There was a suggestion from the Workshop of hatchery rearing and release to the wild of genetically manipulated lobsters for faster growth and earlier maturity.

The potential role of disease and parasites on reducing growth and reproduction and increasing mortality in lobster populations requires further examination (Stewart, this issue). For example, the impact of nemertean egg predators on egg loss (Campbell and Brattey 1986; Wickham, this issue) conceivably could lead to dome-shaped spawning–recruitment curves and host–parasite oscillations (Fogarty and Idoine, this issue). The major egg loss estimates may require a revision of mortality rates for early life stages to balance life tables.

## Models of Stock–Recruitment Relationships

In general, the Workshop concluded that the basic assumptions of biological mechanisms in multistage models should be kept as close to reality as possible. Models should be structured along the functional lines demonstrated by biologists. Indeed, close interdisciplinary collaboration of biologists in modelling with oceanographers, mathematicians, economists, and marine geologists would be useful. Ideally, lobster models might combine reproductive and molt cycles with the influence of temperature on catchability and gear selectivity, and incorporate impacts of culling at sea and bycatch mortality. Consideration of spatial factors, substrate type, and availability of niche sizes at different stages in the life history would also contribute to realism in the resulting model.

Although long-term fishery monitoring programs are useful for time series forecasting models, more research is required to ameliorate understanding of the functional relationships between biotic and abiotic processes in population regulation. Therefore, future studies should investigate (1) the relationships between physical (e.g. oceanic current patterns) factors and larval sources and settlement and (2) density-dependent

mechanisms (e.g. habitat and food limitation, competition, and predation) involved in the early and prerecruit benthic stages. The development of appropriate methodologies to test hypotheses in conjunction with long-term field and laboratory studies to determine how population regulation mechanisms operate on recruitment variability will continue to challenge the ingenuity of scientists for years to come.

## Future Workshops

The meeting suggested that future lobster Workshops consist of small groups focusing on specific topics, e.g. habitat–ecological–fishery interactions or modelling populations from bioeconomic perspectives. The Caribbean region is the center of a major international palinurid lobster fishery. There appear to be a number of problems for improving resource management of this fishery based on scientific principles. These problems and their resolution could be an ideal focus for the next lobster Workshop. A lobster newsletter was advocated and plans are underway to initiate one.

## Acknowledgments

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## References

AIKEN, D. E., AND S. L. WADDY. 1980. Reproductive biology of lobsters, p. 215–276. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

CAMPBELL, A., AND J. BRATTEY. 1986. Egg loss from the American lobster, *Homarus americanus*, in relation to nemertean, *Pseudocarcinonemertes homari*, infestation. Can. J. Fish. Aquat. Sci. 43: 772–780.

COOPER, R., AND J. R. UZMANN. 1980. Ecology of juvenile and adult *Homarus*, p. 97–142. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 2. Academic Press, New York, NY.

HERRNKIND, W. F. 1980. Spiny lobsters: patterns of movement, p. 349–407. *In* J. S. Cobb and B. F. Phillips [ed.] The biology and management of lobsters. Vol. 1. Academic Press, New York, NY.

MOORE, R., AND J. W. MACFARLANE. 1984. Migration of the ornate rock lobster, *Panulirus ornatus* (Fabricius), in Papua, New Guinea. Aust. J. Mar. Freshwater Res. 35: 197–212.

PHILLIPS, B. F., AND J. C. COBB. 1977. Workshop on lobster and rock lobster ecology and physiology. CSIRO, Div. Fish. Oceanogr. (Aust.) No. 7.

## Papers Presented at the Workshop

Authors and titles of papers are in order of presentation. Names of speakers are underlined.

### Session 1
### Introduction

J. E. Stewart (Canada)
Introductory address

### Session 2
### Lobster Fisheries and Recruitment Variability
SESSION CHAIRMAN: J. D. PRINGLE (Canada)

G. P. Ennis (Canada)
Stock definition, recruitment variability, and larval recruitment processes in the American lobster, *Homarus americanus*

G. S. Jamieson (Canada)
Management and recruitment — a review of factors influencing crab year-class strength and the usefulness of predictions

A. A. Fonteles-Filho (Brazil)
Influence of juvenile harvest on stock abundance of *Panulirus argus* (Latreille) and *Panulirus laevicauda* (Latreille) off northeastern Brazil

J. A. Baisre (Cuba)
The Cuban spiny lobster fishery: improvements due to changes in the management system

W. G. Lyons (USA)
Problems and perspectives regarding recruitment of spiny lobsters, *Panulirus argus*, to the south Florida fishery

D. E. Pollock (South Africa)
Population dynamics and management of the fishery for *Jasus lalandii* in South Africa

J. H. Annala (New Zealand)
Yield predictions for the New Zealand rock lobster fishery (Presented by J. Ackroyd)

C. D. MacDonald (USA)
*Puerulus* larval recruitment in the Hawaiian spiny lobster

B. F. Phillips (Australia)
Prediction of commercial catches on the western rock lobster *Panulirus cygnus* George

N. Caputi and R. S. Brown (Australia)
Prediction of recruitment in the western rock lobster *Panulirus cygnus* fishery based on an index of juvenile abundance

### Session 3
### Larval Distribution Dynamics
SESSION CHAIRMAN: B. F. PHILLIPS (Australia)

D. R. Gregory, Jr. and C. L. Coombs (USA)
Is the United States *Panulirus argus* fishery immune to recruitment overfishing?

M. Farmer, J. Ward, and B. Luckhurst (USA)
Predicting destination of larvae and the source of juveniles for the Bermuda spiny lobster (*Panulirus argus*)

J. D. Pringle (Canada)
Speculation on larval recruitment for the California spiny lobster (*Panulirus interruptus*)

B. F. Phillips and P. S. McWilliam (Australia)
Ocean circulation patterns and recruitment of spiny lobsters

J. R. McConnaugha (USA)
Dynamics of blue crab (*Callinectes sapidus*) distribution and recruitment

K. Brander (United Kingdom)
A preliminary account of the distribution and dynamics of larvae of *Nephrops norvegicus* in the Irish Sea (Presented by R. C. A. Bannister)

C. Hudon and P. Fradette (Canada)
Horizontal and vertical distribution of lobster larvae (*Homarus americanus*) off the Magdalen Islands, Gulf of St. Lawrence

G. Harding, J. D. Pringle, and P. Vass (Canada)
Verticle migration by lobster (*Homarus americanus*) larvae

R. W. Elner (Canada)
Vertical migration behavior of lobster, *Homarus americanus*, larvae in the laboratory

G. P. Ennis (Canada)
Swimming ability of larval American lobsters, *Homarus americanus*, in flowing water

S. D. Sulkin (USA)
Application of experimental studies of larval behavior to fisheries problems

### Session 4
### Behavior and Movement
SESSION CHAIRMAN: W. F. HERRNKIND (USA)

A. Campbell and D. S. Pezzack (Canada)
Overview of movement patterns, relative distribution and abundance of lobsters, *Homarus americanus*, in the Bay of Fundy and off southwest Nova Scotia

D. S. Pezzack and D. R. Duggan (Canada)
Lobster (*Homarus americanus*) migrations on the southest Scotian Shelf

T. L. Meyer, J. R. Uzmann, R. A. Cooper, and M. J. Fogarty (USA)
Preliminary report on lobster tagging studies in central Gulf of Maine

P. Daniel, R. Bayer, and J. Krouse (USA)
Movements of large tagged female American lobsters released near the Maine coast in fall of 1983

J. S. Cobb (USA)
Larval lobster (*Homarus americanus*) behavior: the effect of age and experience in the fourth stage

J. Booth (New Zealand)
A recruitment mechanism for the packhorse rock lobster *Jasus verreauxi* in New Zealand

R. N. Lipcius and W. F. Herrnkind (USA)
Reproductive patterns, movements and recruitment in Pal-Palinurid lobsters

J. M. Marx (USA)
Recruitment and settlement of pueruli in south Florida

B. F. Phillips (Australia)
The puerulus stage of the spiny (rock) lobster and its ability to locate the coast

### Session 5
### Recruitment Enhancement
SESSION CHAIRMAN: G. Y. CONAN (Canada)

G. Y. Conan (Canada)
Review of methods of recruitment enhancement

J. Kittaka (Japan)
Lobster stocking experience in Japan

A. E. Howard, T. W. Beard, and J. F. Wickins (United Kingdom)
Progress towards the enhancement of English stocks of lobster (*Homarus gammarus*, L.)

R. S. Brown and N. Caputi (Australia)
Factors adversely affecting the recapture and growth of undersize western rock lobster *Panulirus cygnus* and ways of solving the problem

J. H. Hunt (USA)
Injury induced reduction in recruitment to the south Florida spiny lobster fishery

D. L. Miller (USA)
Spiny lobster (*Panulirus argus*) fisheries and artificial habitats: increasing the yields by merely concentrating stocks?

R. C. A. Bannister (United Kingdom)
Estimating the survival of microtagged hatchery-reared lobsters in the wild

J. Lorec (France)
Restocking experience in France

**Session 6**
**Ecology of Population Structure**
SESSION CHAIRMAN: J. S. COBB (USA)

C. J. Chapman, N. Bailey, and G. Howard (United Kingdom)
Density, growth and recruitment of *Nephrops norvegicus* in relation to environmental factors

R. F. Ford, B. F. Phillips, and L. M. Joll (USA–Australia)
Influences of population density on growth, mortality and nutritional state of juvenile lobsters (*Panulirus cygnus*)

D. E. Barshaw and D. R. Bryant (USA)
Early juvenile stages of the lobster, *Homarus americanus*: behavior, growth, and survival in naturalistic environments

B. Michaud (USA)
Composition and production of macrobenthic invertebrate communities and food resources of the American lobster, *Homarus americanus*

R. W. Elner and A. Campbell (Canada)
Natural diet of juvenile lobsters, *Homarus americanus*, from a sea urchin dominated barren ground on the Atlantic coast of Canada

R. A. Richards and J. S. Cobb (USA)
Relative body size and competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*)

P. Lawton (Canada)
Diel activity and foraging behavior of juvenile lobsters, *Homarus americanus*

**Session 7**
**Factors Affecting Growth and Reproduction**
SESSION CHAIRMAN: D. E. AIKEN (Canada)

D. E. Aiken and S. L. Waddy (Canada)
The influence of environment on growth, reproduction and eventual recruitment of the American lobster

L. S. Quackenbush (USA)
Hormonal regulation of growth and reproduction in *Panulirus argus*

D. E. Aiken and S. L. Waddy (Canada)
Growth of the vasa deferentia of mature American lobsters: lack of evidence for cyclic seasonal changes associated with reproduction

D. E. Aiken and S. L. Waddy (Canada)
Allometric growth and onset of maturity in male American lobsters

A. H. Hines (USA)
Geographic variation in growth and size at maturity in the life histories of brachyuran crabs

J. Atema, D. Cowan, R. H. Elgin, E. B. Karnofsky, D. McPhie, and S. Oleszko-Szuts (USA)
Behavior associated with courtship and mating in *Homarus americanus*

S. L. Waddy and D. E. Aiken (Canada)
Multiple fertilization and consecutive-year spawning: mechanisms for increasing reproductive contribution of large female American lobsters

P. Briones-Fourzan (Mexico)
Aspects of the reproduction of *Panulirus gracilis* Streets and *P. inflatus* (Bouvier) in Guerrero, Mexico

D. E. Wickham (USA)
The appearance and spread of epidemic outbreaks of nemertean crab-egg predators and their role in host egg mortality

A. Campbell and J. Brattey (Canada)
Egg loss from the lobster, *Homarus americanus*, in relation to nemertean, *Pseudocarcinonemertes homari*, infestation

B. MacKenzie (Canada)
Temperature-controlled development of larval *Homarus americanus*: an update

M. D. Eagles, D. E. Aiken, and S. L. Waddy (Canada)
Influence of light and food on survival, growth and development rate of larval American lobsters

E. Lozano-Alvarez and P. Briones-Fourzan (Mexico)
Growth patterns of *Panulirus gracilis* Streets of the Mexican Pacific Coast

J. M. Capuzzo, G. G. Sasaki, and P. Biesiot (USA)
Nutritional and bioenergetic considerations in the early development of the American lobster, *Homarus americanus*

J. D. Castell and J. C. Kean (Canada)
Nutritional aspects that may affect the recruitment of the American lobster

**Session 8**
**Models of Stock–Recruitment Relationships**
SESSION CHAIRMAN: M. J. FOGARTY (USA)

J. F. Caddy (Italy)
Modelling stock–recruitment processes in Crustacea, some practical and theoretical perspectives

L. W. Botsford (USA)
Effects of environmental forcing on age-structured populations: northern California dungeness crab (*Cancer magister*) as an example

W. T. Momot (Canada)
The influence of life-history events in the recruitment of freshwater crayfish

R. C. A. Bannister and J. T. Addison (United Kingdom)
Stock recruitment relationships and the long-term dynamics of the European lobster (*Homarus gammarus* L.)

J. T. Addison (United Kingdom)
How recruitment processes could influence the relationship between size composition and fishing effort in crustacean fisheries

R. K. Mohn and A. Campbell (Canada)
A spatially distributed model of lobster recruitment

M. J. Fogarty (USA)
Implications of alternative stock–recruitment relationships for the stability of lobster populations

## Poster Papers Presented at the Workshop

J. Attard, P. Fradette, and C. Hudon (Canada)
Egg development and reproductive potential of female lobsters *Homarus americanus*, in different areas of the Magdalen Islands, Gulf of St. Lawrence

J. Booth (New Zealand)
A recruitment mechanism for *Jasus edwardsii* in New Zealand

J. Booth (New Zealand)
Aspects of the ecology and distribution of *Jasus edwardsii* larvae near Gisborne, New Zealand

S. F. Bossy (United Kingdom)
An investigation into the seasonality of egg production of the European lobster (*Homarus gammarus*) around Jersey, Channel Islands

G. Carrasco-Zanini and E. Lozano-Alvarez (Mexico)
Homing and home range of *Panulirus guttatus* in the Mexican Caribbean

G. Charmantier, M. Charmantier-Daures, and W. W. Young-Lai (France–Canada)
Lethal and sublethal effects of potash brine on different stages of the lobster, *Homarus americanus*

G. Y. Conan, M. Comeau, and M. Moriyasu (Canada)
Morphometrics of male lobsters in the Gulf of St. Lawrence, incidence of maturity, incidence of geographical variability

D. Cowan and J. Atema (USA)
A bioassay for female sex pheromones in the lobster, *Homarus americanus*

D. R. Gregory, Jr. and R. F. Labisky (USA)
Long-distance movements of the spiny lobster *Panulirus argus* in south Florida

Y. Hénocque (France)
Age and intermolt stage identification of the decapods, *Homarus gammarus* and *Nephrops norvegicus*, based on observations of external and internal parts of the animal
(Presented by D. Latrouite)

A. E. Howard (United Kingdom)
Review of the influence of substrate on the population structure of English stocks of lobster (*Homarus gammarus*, L.)

D. Latrouite (France)
Lobster management in France: past and present

D. E. Maynard, Y. Chaisson, and G. Y. Conan (Canada)
Geographical and seasonal variation in the abundance of ovigerous female lobsters in the Gulf region

M. Moriyasu and P. Mallet (Canada)
Maturity of female lobster in northern Northumberland Strait and in Malpeque Bay

J. H. Nichols, D. B. Bennett, D. J. Symonds, and R. Grainger (United Kingdom)
Estimation of the stock size of adult *Nephrops norvegicus* (L.) from larval surveys in the western Irish Sea in 1982
(Presented by R. C. A. Bannister)

B. F. Phillips and A. F. Pearce (Australia)
Larval recruitment of western rock lobster *Panulirus cygnus* George and the role of the southern oscillation and the Leeuwin current

G. Roach (Canada)
Survivorship, growth and behavior of juvenile lobsters, *Homarus americanus*, in controlled environments in nature

F. Sardá (Spain)
Age and growth in *Nephrops norvegicus*

F. Sardá and P. Abello (Spain)
Distribution, abundance and fecundity of Norway lobster (*Nephrops norvegicus*, L.) in the Western Mediterranean Sea

G. J. Sharp, L. Boston, and D. M. Tremblay (Canada)
The effect of tank size on settlement behaviour of stage IV *Homarus americanus*

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53 — Chris Chubb, 54 — Robert Elner, 55 — Brian MacKenzie, 56 — Gareth Harding, 57 —
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70 — Robert Bayer, 71 — David Miller.

*Attendees not in picture*: Peter Daniel, Antonio Fontelles-Filho, Kevin Kelly, Jay Krouse, Dona

en Jamieson, 6 — James Stewart, 7 — Raj Misra, 8 — Michael Fogarty, 9 — Greg Roach, 10 — ulio Baisre, 15 — Peter Lawton, 16 — Richard Ford, 17 — John Caddy, 18 — Craig MacDonald, — Stanley Cobb, 24 — William Herrnkind, 25 — Simon Bossy, 26 — Bruce Phillips, 27 — Colin a Briones-Fourzan, 32 — Patricia Biesiot, 33 — Julian Addison, 34 — Judy Capuzzo, 35 — Mary 39 — Brian Michaud, 40 — Anne Richards, 41 — David Aiken, 42 — Michael Eagles, 43 — Steve e, 48 — Jack Ward, 49 — Walter Momot, 50 — Jo Akroyd, 51 — Sara Ellis, 52 — Jiro Kittaka, g, 57 — Rhys Brown, 58 — Joël Lorec, 59 — Irene Pohle, 60 — Douglas Pezzack, 61 — John Hudon, 66 — Daniel Latrouite, 67 — Colin Chapman, 68 — David Scarratt, 69 — Rom Lipcius,

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# ANNOUNCEMENTS/AVIS

## C.C.F.F.R. – C.C.R.P.
## Vancouver, 5–6 January, 1987

***Preliminary Program and Call for Papers***

This year's program will begin on Monday, January 5, with the Stevenson lecture, to be presented by Dr. Bill Leggett of McGill University. The Stevenson lecture will be followed by two contributed papers sessions organized around specific themes: (1) Climate and Oceanography and its Effects on Fisheries and (2) Ecology and Population Dynamics of Forage Species. Tuesday, January 6, will begin with an invited papers session: The Biology of Little Known and Unusual Canadian Fishes. This session is being convened by M. C. Healey. The invited papers session will be followed by a poster session, and in the afternoon by a contributed papers session without theme. M. C. Healey is in charge of the overall scientific program, Jake Schweigert is coordinating the contributed papers sessions (all three), and Laura Richards is coordinating the poster session.

This is a ***Call for Abstracts*** for the three contributed papers sessions and the poster session. Type your abstract (maximum 200 words, single spaced). In particular, we want to hear from those of you who want to contribute to one of the sessions having a particular theme. Depending on the number of papers received, we may have to rearrange the sessions. Please forward abstracts for the contributed papers sessions to Jake Schweigert and indicate on your abstract in which session you think the paper belongs. Abstracts for the poster session should be forwarded to Laura Richards. General enquiries should be sent to Mike Healey. Jake, Laura, and Mike are all at the Department of Fisheries and Ocean, Pacific Biological Station, Nanaimo, B.C. V9R 5K6. Deadline for abstracts is November 30, 1986. Earlier submission would, however, be appreciated.

The meetings will be held at the Delta River Inn in Richmond. Dr. G. Geen, Biology Department, Simon Fraser University, is in charge of local arrangements. Contact him for further information about hotel rates, etc.

## Conférence canadienne relative à la recherche sur les pêches
## Vancouver, les 5 et 6 janvier 1987

***Programme préliminaire et appel de documents***

Le programme de cette année débutera le lundi 5 janvier avec la conférence Stevenson, qui sera présentée par le Dr Bill Leggett de l'Université McGill. La conférence Stevenson sera suivie de deux séances de présentation de documents organisées autour de thèmes précis : (1) le climat et l'océanographie et ses effets sur les pêches et (2) écologie et dynamique de population d'espèces fourrage. Le mardi 6 janvier débutera avec une séance d'exposés de conférenciers invités : la biologie de poissons du Canada inhabituels et peu connus. Cette séance est convoquée par M. C. Healey et sera suivie par après d'une séance d'affichage et dans l'après-midi d'une séance de présentation de documents sans thème. M. C. Healey est la personne responsable de l'ensemble du programme scientifique, Jake Schweigert coordonne les séances de présentation de documents (les trois), tandis que Laura Richards coordonne la séance d'affichage.

Par la présente, on ***demande des résumés*** pour les trois séances de présentation de documents et pour la séance d'affichage. Veuillez dactylographier votre résumé (maximum de 200 mots à simple interligne). En particulier, nous désirons avoir des nouvelles de ceux d'entre vous qui veulent participer à l'une des séances ayant un thème donné. Selon le nombre de documents reçus, il est possible que nous devions remanier les séances. Veuillez faire parvenir les résumés pour les séances de présentation de documents à Jake Schweigert et indiquer sur votre résumé à quelle séance vous pensez que le document se rattache. Les résumés pour la séance d'affichage doivent être envoyés à Laura Richards. Les demandes de renseignements généraux doivent être adressées à Mike Healey. Jake, Laura et Mike travaillent tous pour le ministère des Pêches et des Océans, à la Station de biologie du Pacifique, Nanaimo (C.-B.) V9R 5K6. La date limite pour les résumés est le 30 novembre 1986. Cependant, nous aimerions les recevoir plus tôt.

Les réunions auront lieu au Delta River Inn, à Richmond. Le Dr G. Geen, département de biologie, Université Simon Fraser, est chargé de faire les arrangements au niveau local. Communiquez avec lui si vous désirez de plus amples informations au sujet des tarifs d'hôtel, etc.

# COMING NEXT MONTH/À PARAÎTRE LE MOIS PROCHAIN

## Articles


Virtual population analysis (VPA) equations for nonhomogeneous populations, and a family of approximations including improvements on Pope's cohort analysis **A. D. MacCall**

Benthic microfaunal production in the Bay of Fundy and the possible effects of a tidal power barrage at Economy Point – Cape Tenny **D. J. Wildish, D. L. Peer, and D. A. Greenberg**

Analysis of long-term ecological data using categorical time series regression **K. A. Rose, J. K. Summers, R. A. Cummins, and D. G. Heimbuch**

Nickel ion requirements for autotrophic growth of several marine microalgae with urea serving as nitrogen source **L. Oliveira and N. J. Antia**

Family size and effective population size in a hatchery stock of coho salmon (*Oncorhynchus kisutch*) **R. C. Simon, J. D. McIntyre, and A. R. Hemmingsen**

Use of hatchery coho salmon (*Oncorhynchus kisutch*) presmolts to rebuild wild populations in Oregon coastal streams **T. E. Nickelson, M. F. Solazzi, and S. L. Johnson**

Conductivity–temperature standardization and dissolved solids estimation in a meromictic saline lake **K. J. Hall and T. G. Northcote**

Adaptive divergence of trophic phenotype among freshwater populations of the threespine stickleback (*Gasterosteus aculeatus*) **P. A. Lavin and J. D. McPhail**

Seasonal dynamics of phosphorus partitioning and export in two streams in Alberta, Canada **N. Munn and E. Prepas**


## Reviews/Synthèses


Algal picoplankton from marine and freshwater ecosystems: a multidisciplinary perspective **J. G. Stockner and N. J. Antia**

Existence de populations uricotéliques chez *Abra abra* et *Dreissena polymorpha* (Bivalves Eulamellibranches) **F. Secchi et M. Martoja**


## Notes


Sequential tests for infectious hematopoietic necrosis virus in individuals and populations of sockeye salmon (*Oncorhynchus nerka*) **D. Mulcahy and R. Pascho**

Selective predation by *Procladius* in an arctic Alaskan lake **A. E. Hershey**

Prediction of emergent and floating-leaved macrophyte cover in Central Swedish lakes **V. H. Smith and M. Wallsten**

Diel vertical migrations and horizontal distributions of *Limnocalanus macrurus* and *Senecella calanoides* (Copepoda, Calanoida) in lakes of southern Ontario in relation to planktivorous fish **J. C. H. Carter and K. A. Goudie**

Survival from sea lamprey (*Petromyzon marinus*) predation by two strains of lake trout (*Salvelinus namaycush*) **W. D. Swink and L. H. Hanson**

Prediction of angler success in an Atlantic salmon, *Salmo salar*, fishery two fishing seasons in advance **P. M. Ryan**


## Letters and comments/Lettres et commentaires


Some remarks on "Model of monthly marine growth and natural mortality for Babine Lake sockeye salmon (*Oncorhynchus nerka*)" by Furnell and Brett **M. D. McGurk**

Reply **D. J. Furnell and J. R. Brett**

**Recruitment of packhorse rock lobster *Jasus verreauxi* in New Zealand** J. D. Booth **2212–2220**
**Settlement of spiny lobster, *Panulirus argus*, pueruli in south Florida: an evaluation from two perspectives** J. M. Marx **2221–2227**
**Movements of the spiny lobster *Panulirus argus* in south Florida** D. R. Gregory, Jr. and R. F. Labisky **2228–2234**

Session 5: Recruitment Enhancement
(Chairman: G. Y. Conan)

**Conservation of recruitment of the western rock lobster (*Panulirus cygnus*) by improving survival and growth of undersize rock lobsters captured and returned by fishermen to the sea** R. S. Brown and N. Caputi **2236–2242**
**Factors affecting growth and maturation of spiny lobsters, *Panulirus argus*, in the Florida Keys** J. H. Hunt and W. G. Lyons **2243–2247**

Session 6: Ecology of Population Structure
(Chairman: J. S. Cobb)

**Competition for shelter between lobsters (*Homarus americanus*) and Jonah crabs (*Cancer borealis*): effects of relative size** R. A. Richards and J. S. Cobb **2250–2255**

Session 7: Factors Affecting Growth and Reproduction
(Chairman: D. E. Aiken)

**Environmental influence on recruitment of the American lobster, *Homarus americanus*: a perspective** D. E. Aiken and S. L. Waddy **2258–2270**
**Crustacean endocrinology, a review** L. S. Quackenbush **2271–2282**
**Review of sexual selection and chemical communication in the lobster, *Homarus americanus*** J. Atema **2283–2290**
**Multiple fertilization and consecutive spawning in large American lobsters, *Homarus americanus*** S. L. Waddy and D. E. Aiken **2291–2294**
**Epizootic infestations by nemertean brood parasites on commercially important crustaceans** D. E. Wickham **2295–2302**
**Influence of light and food on larval American lobsters, *Homarus americanus*** M. D. Eagles, D. E. Aiken, and S. L. Waddy **2303–2310**
**Nutritional and bioenergetic considerations in the development of the American lobster *Homarus americanus*** G. C. Sasaki, J. M. Capuzzo, and P. Biesiot **2311–2319**
**Evaluation of the role of nutrition in lobster recruitment** J. D. Castell and J. C. Kean **2320–2327**

Session 8: Models of Stock–Recruitment Relationships
(Chairman: M. J. Fogarty)

**Modelling stock–recruitment processes in Crustacea: some practical and theoretical perspectives** J. F. Caddy **2330–2344**
**Effects of environmental forcing on age-structured populations: northern California Dungeness crab (*Cancer magister*) as an example** L. W. Botsford **2345–2352**
**Effect of assumptions about the stock–recruitment relationship on a lobster (*Homarus gammarus*) stock assessment** R. C. A. Bannister and J. T. Addison **2353–2359**
**Density-dependent mortality and the relationship between size composition and fishing effort in lobster populations** J. T. Addison **2360–2367**
**Recruitment dynamics in an American lobster (*Homarus americanus*) population** M. J. Fogarty and J. S. Idoine **2368–2376**

Session 9: Implications of the Workshop

**Summary of Session 2** J. D. Pringle **2378–2379**
**Summary of Session 3** B. F. Phillips **2380–2382**
**Summary of Session 4** W. F. Herrnkind **2383**
**Summary of Session 5** G. Y. Conan **2384–2388**
**Summary of Session 6** J. S. Cobb **2389–2390**
**Summary of Session 7** D. E. Aiken **2391**
**Summary of Session 8** M. J. Fogarty **2392–2393**
**Summary of Session 9** J. F. Caddy and A. Campbell **2394–2396**
**Papers presented at the workshop** **2397–2399**
**Poster papers presented at the workshop** **2399**
**List of participants** **2399–2402**

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**Announcements / Avis** **2403**
**Coming next month / À paraître le mois prochain** **2404**

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International Workshop on Lobster Recruitment

**Introduction to the International Workshop on Lobster Recruitment** — A. Campbell — **2064–2065**

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**Introductory address** — J. E. Stewart — **2068–2069**

**Dedication** — J. D. Pringle — **2070**

Session 2: Lobster Fisheries and Recruitment Variability
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**Stock definition, recruitment variability, and larval recruitment processes in the American lobster, *Homarus americanus*: a review** — G. P. Ennis — **2072–2084**

**Implications of fluctuations in recruitment in selected crab populations** — G. S. Jamieson — **2085–2098**

**Problems and perspectives regarding recruitment of spiny lobsters, *Panulirus argus*, to the south Florida fishery** — W. G. Lyons — **2099–2106**

**Review of the fishery for and biology of the Cape rock lobster *Jasus lalandii* with notes on larval recruitment** — D. E. Pollock — **2107–2117**

**Recruitment of the puerulus of the spiny lobster, *Panulirus marginatus*, in Hawaii** — C. D. MacDonald — **2118–2125**

**Prediction of commercial catches of the western rock lobster *Panulirus cygnus*** — B. F. Phillips — **2126–2130**

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